NEURONAL ORGANIZATION WITHIN THE MAMMALIAN DORSAL LATERAL GENICULATE COMPLEX AND ADJACENT PULVINAR NUCLEI: A COMPARATIVE APPROACH

by

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Declaration

I declare that the work described in this thesis is my own and has not been previously submitted at any University for any degree.

Curriculum Vitae

The author graduated in Physiology and Biochemistry at the University of Southampton in 1973. The period 1973-1976 was spent in the Research Department of Communication at the University of Keele studying for the degree of Ph.D.

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ABSTRACT

This dissertation attempts to understand the organization of some of the nuclei which constitute the mammalian visual thalamus through an electrophysiological and histological investigation of the cat and rat aided by an evaluation of comparative neuro- anatomical and physiological literature.

The introduction initially reviews the anatomy and physiology of the cat's visual system. Later a review of comparative aspects provides a background for the evaluation of the experimental results in a comparative context.

Responses of cells in the cat's dorsal lateral geniculate complex, comprising the laminated lateral geniculate and medial interlaminar (MIN) nuclei, were investigated in paralysed cats, lightly anaesthetized with either pentobarbitone or N_2O/O_2 supplemented with pentobarbitone. Geniculate cells were initially classified as sustained or transient according to their response properties. This revealed a differential distribution of receptive field types within the LGNd complex, and evidence of laminar organization in the MIN.

Later cells were further classified as 'brisk' or 'sluggish', sustained or transient according to their response properties providing additional evidence for a differential distribution of 'brisk' and 'sluggish' cell types within the LGNd complex.

Responses of cells in the LGNd complex to textured 'visual noise' were also investigated. On-centre/off-centre and sustained/ transient cell types in the LGNd complex did not appear to be differentiated by their responses to visual noise as are simple and complex cells in the striate cortex.

A preliminary investigation of the response properties and visuotopic organization of cells in the feline extrageniculate visual thalamus was attempted. It was found that cytoarchitecturally defined thalamic regions do not essentially delineate functional (visuotopically organized) regions.

The response properties of cells in the rat's LGNd (with regard to the sustained/transient classification) and pulvinar were investigated. These results were compared with the neuronal organization found in the cat.

In the discussion an overview of the experimental results is provided and the functional significance of the neuronal organization found in the mammalian LGNd complex and pulvinar-complex is discussed.

Abbreviations

LGNd	dorsal lateral geniculate nucleus
LGNv	ventral lateral geniculate nucleus
PGN	perigeniculate nucleus
MIN	medial interlaminar nucleus
CIN	central interlaminar nucleus

Cell type identification (LGNd complex):

T^b	'brisk' transient
S^b	'brisk' sustained
T^s	'sluggish' transient
S^s	'sluggish' sustained
M	mixed properties
O	other types
U	Unclassified

Cell identification number (e.g. 4509) - the first two digits signify the experimental number (e.g. experiment 45), and the second two digits the cell number (e.g. cell 09).

The symbols (on), (off) or (on-off) following the cell identification number refer to the centre type of the cell if responsive to flashed stimuli.

CONTENTS

Acknowledgements

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INTRODUCTION:

This dissertation is an attempt to understand the organization of some of the nuclei which constitute the mammalian visual thalamus through an electrophysiological and histological investigation of the cat and rat aided by an evaluation of comparative neuro-anatomical and physiological literature.

The initial portion of the introductory review is concerned with the anatomy and physiology of the cat's visual system. Later a brief review of comparative aspects will provide a background for the evaluation of the experimental results in a comparative context.

1.1. LGNd-complex: Histological organization:

The feline lateral geniculate nucleus (LGN) comprises a complex of nuclei divisible primarily into dorsal (LGNd) and ventral (LGNv) divisions, both of which may be further sub-divisible.

The LGNv basically consists of an external magnocellular layer and an internal parvocellular layer, both of which may undergo further species specific differentiation (Niimi et al, 1963). The LGNv receives afferent input from the retina, visual cortex and superior colliculus (Hayhow, 1958; Altman and Carpenter, 1961; Laties and Sprague, 1966; Garey and Powell, 1968; Kawamura et al, 1974).

The dorsal division of the cat lateral geniculate nucleus (LGNd) may be considered to comprise of at least two major subdivisions, the laminated portion and the medial interlaminar nucleus (MIN). The MIN is considered by some authors (e.g. Thuma, 1928; Hayhow, 1958) to be the medial component of the central interlaminar nucleus (CIN), a group of large cells scattered between the laminae of the laminar LGNd (Fig. 1).

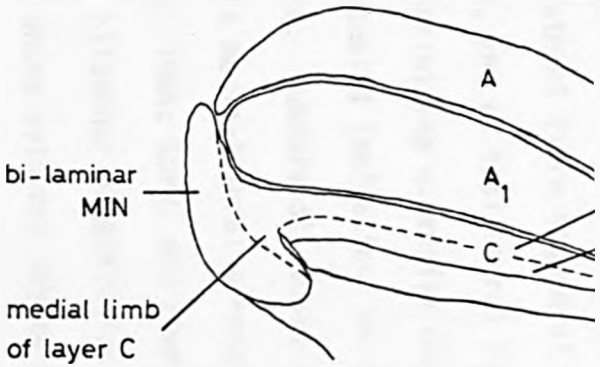
Capping the dorsal margin of the LGNd complex is a scattered layer of cells - the perigeniculate nucleus (NPG). The NPG receives a sparse retinal input (Laties and Sprague, 1966) and projections from areas 17 and 18 (Kawamura et al, 1974).

LGNd:

The most widely adopted nomenclature used for describing the laminated LGNd is that proposed by Thuma (1928) for a trilaminated structure with contralaterally recipient layers A and B, and an ipsilateral layer A_1. The laminar cyto-morphology may be characterized dorso-ventrally as follows: Laminae A and A_1 comprise a fairly uniform distribution of small (10-20μm), medium (20-25μm) and large (30-40μm) cells; while lamina B comprises small to medium sized cells. Separating the laminae, in particular laminae A_1 and B, are two interlaminar plexi containing scattered large cells (the CIN). A recent re-evaluation of the distribution of retinal afferents to the LGNd considers the B lamina to be further subdivisible into contralateral (C and C_2) and ipsilateral (C_1) recipient layers (Guillery, 1970; Hickey & Guillery, 1974). This description is essentially similar to that of Rioch (1929) who defined the LGNd as a four-layered structure, the principalis anterior, principalis posterior, and magnocellularis corresponding to Guillery's layers A, A_1, and C, and the parvocellular lamina, whose sub-division can only be revealed by retino-geniculate degeneration patterns of autoradiographic techniques, corresponding to layers C_1, C_2 and C_3.

The difficulties of relating the various accounts of laminar organization appear to be largely due to different methods of identification and terminology of the individual laminae. The description of Guillery (1970) appears to be the most rigorous to date and is readily equatable with previous studies. Electrophysiological mapping studies have

FIG. 1. A comparison of the nomenclature used by different authors in relation to a transverse section through the cat's LGNd complex. The modified nomenclature after Guillery (1970) is that adopted in this thesis.

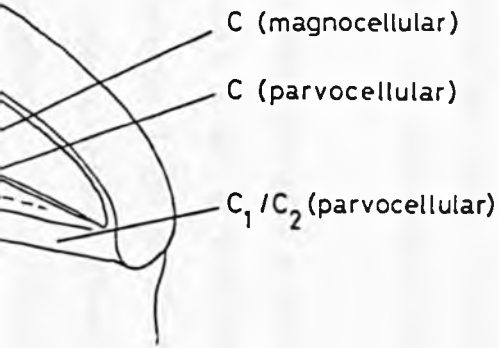


layer nomenclature

driving eye	layer [1]	Thuma (1928)
contralat.	A	A
ipsilat.	A_1	A_1
contralat.	C (magno)	CIN
	C (parvo)	
ipsilat.	C_1	B
contralat.	C_2	

1 modified after Guillery (1970)

1 mm



Rioch (1929)	Kanaseki (1958)
principalis anterior	lamina I
principalis posterior	lamina II
magnocellularis	lamina III
parvocellularis	lamina IV

confirmed Guillery's five-layered description of the laminated LGNd (Daw and Pearlman, 1970; Sanderson, 1971; Kaas et al, 1971).

MIN:

The medial interlaminar nucleus (MIN), a cluster of large cells situated adjacent and medial to the laminated LGNd, was first described by Thuma (1928) who considered that it constituted a separate component of the LGNd.

Hayhow (1958) provided a more detailed account of the MIN and established that it was a recipient of optic tract fibres, and from the results of unilateral eye enucleation suggested a trilaminated organization arranged in a medio-lateral direction (cf. laminated LGNd with a dorso-ventral arrangement). This laminar organization was revealed as bands of contralateral fibre degeneration along the medial and lateral margins of the MIN, and as ipsilateral band situated centrally within the MIN, the bands exhibiting extensive overlap. This may be regarded as an example of 'concealed lamination' in that it cannot be seen in normal histological sections. Authors of subsequent anatomical studies have provided support for this medio-lateral arrangement (Stone and Hansen, 1966; Laties and Sprague, 1966; Garey and Powell, 1968).

A bilaminar organization within the MIN was proposed by Guillery (1970) whose evidence may be summarized as follows:

(i) The lateral, vertically oriented bar receiving contralateral fibres (Hayhow, 1958) should be considered as the medial limb of layer C of laminated LGNd, as deduced from the fibre degeneration pattern and apparent continuity of these cells with those of layer C.

(ii) Re-evaluation of degeneration patterns following localized retinal lesions (Stone and Hansen, 1966; Laties and Sprague, 1966; Garey and Powell, 1968) reveals that a lesion in the contralateral nasal retina results in only one focus of degeneration and not two as predicted from Hayhow's description (1958).

1.2. LGNd-complex: Retinotopic organization:

The early anatomical studies of Brouwer et al (1923) and Overbosch (1928) were able to demonstrate a topographical projection from the retina to the LGNd following retinal lesions.

Bishop et al (1962) provided the first electrophysiological mapping investigation of retinotopic organization within the laminated LGNd, plotting the visual directions of receptive fields of single geniculate neurones (the visual direction being expressed in terms of two angles, azimuth and elevation). This study also provided supportive evidence for the trilaminar organization of the laminated LGNd with laminae A and B driven contralaterally and laminae A_1 ipsilaterally.

Seneviretne and Whitteridge (1962) and Bishop (1965) reported a second mirror-image representation of the visual field located at the medial edge of the laminated LGNd, identical to the area occupied by the MIN. A subsequent study (Kinston et al, 1969) explored the projection of the visual field to the medial edge of the laminated LGNd and adjacent nuclei in further detail and demonstrated the complete representation of the visual field in the MIN, with the exception of the upper periphery; the lateral and medial margins of the MIN contained the central and peripheral regions of the visual field respectively. Kinston et al noted that although contralaterally and ipsilaterally driven cells tended to be

recorded in clusters they found no evidence for the trilaminar, medio-lateral arrangement suggested by anatomical studies.

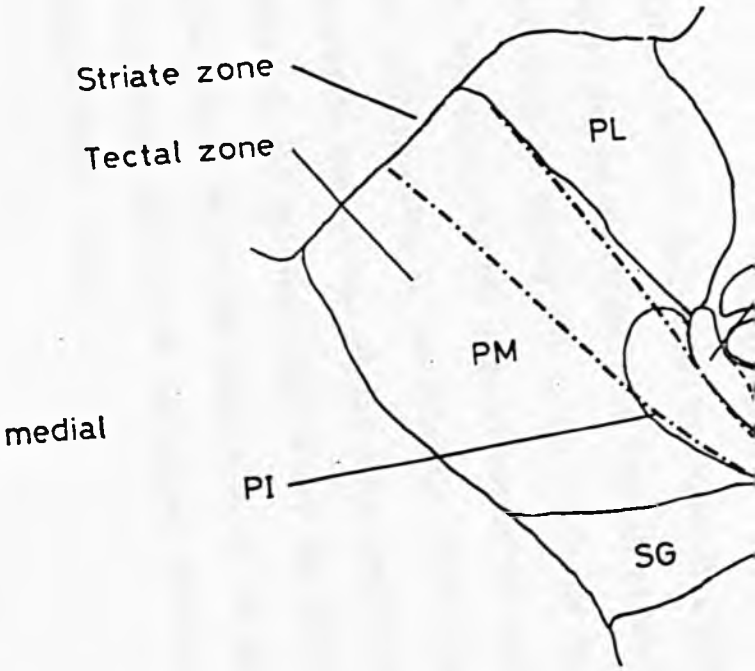
A complete and detailed description of the projection of the visual field to the laminated LGNd and MIN was prepared by Sanderson (1971), relating the electrode recording sites of a given cell in the laminated LGNd or MIN to the position of its receptive field in the visual field. Like previous authors, Sanderson also failed to provide support for the laminar organization postulated anatomically. This study additionally provided confirmation of Daw and Pearlman's electrophysiological report (1970) of ipsilaterally driven cells situated ventrally in laminae B of laminated LGNd (Guillery's layer C_1), so supporting the five-layered laminated LGNd structure suggested by Guillery (1970).

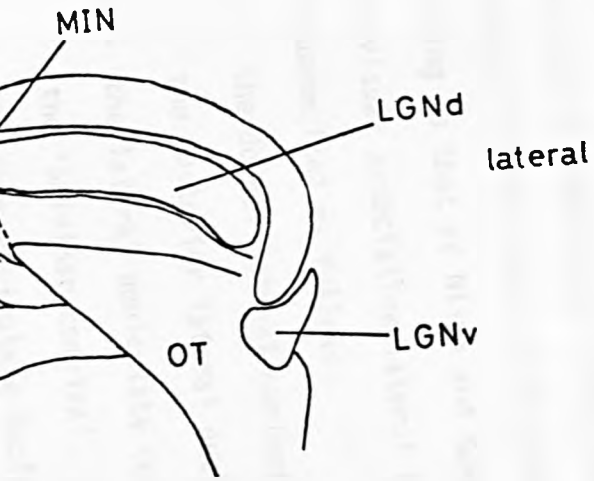
The electrophysiological mapping of the visual field representation in the laminated LGNd and MIN has also been confirmed by many anatomical studies (Moore et al, 1964; Laties and Sprague, 1966; Stone and Hansen, 1966; Garey and Powell, 1968). The resolution of anatomical maps are not as precise as those obtained by electrophysiological methods, largely due to the problem that even very small retinal lesions may interfere with optic fibres of passage, resulting in a larger effective area of damage.

The lateral and posterior thalamic nuclear groups:

1.3. Situated medially to the LGNd-complex are a group of nuclei, which constitute the lateral and posterior thalamic nuclear groups, with anatomically and/or physiologically demonstrable visual associations. However the range of nomenclature used to describe these nuclei in mammals is confusing and frequent reference to Fig. 2 will aid the following comparison. Niimi and Kuwahara's (1973) recent comparative

FIG. 2. Diagram of the nuclei constituting the cat's visual thalamus (the lateral and posterior nuclear groups and the lateral geniculate complex). Nomenclature after Niimi and Kuwahara (1973): PI = inferior pulvinar; PM = medial pulvinar; PL = lateral pulvinar; SG = suprageniculate nucleus; LGNd = dorsal lateral geniculate nucleus; LGNv = ventral lateral geniculate nucleus; MIN = medial interlaminar nucleus; OT = optic tract.


Striate zone
Tectal zone
PL
PM
medial
PI
SG


MIN
LGNd
lateral
OT
LGNv

cytoarchitectural study of the mammalian dorsal thalamus is a significant attempt to unify the variety of classification in current usage. Their description for the cat is compatible with most earlier studies and with the stereotaxic atlases of Jasper and Ajmone-Marsan (1954) and Snider and Niemer (1963). The cytoarchitectural nomenclature to be adopted throughout this thesis is according to that of Niimi and Kuwahara (1973) and the nuclei constituting the visual associative lateral and posterior thalamic nuclear groups may be summarized as follows:

Lateral nuclear group	-	the dorsal lateral nucleus (Ldn).
		the posterior lateral nucleus (Ldn).
Posterior nuclear group	-	the lateral geniculate complex.
		the 'pulvinar complex'.
		the suprageniculate nucleus (SG).

The organization of the LGN-complex has been discussed earlier (1.1.). The pulvinar-complex may be differentiated into three divisions: the inferior pulvinar which is equivalent to the posterior nucleus (PN); the medial pulvinar, equivalent to the lateral posterior nucleus (LP); and the lateral pulvinar corresponding to the pulvinar (Pul). The suprageniculate nucleus corresponds to the nucleus of the same name in the stereotaxic atlases. Anterior to the pulvinar-complex are the dorsal lateral and posterior lateral nuclei which are comparable to the dorsal lateral nucleus and the anterior portion of the lateral posterior nucleus (LP) of Jasper and Ajmone-Marsan (1954).

1.3.1. Pulvinar-complex: Retinotopic organization:

Unlike the laminated LGNd and MIN the nuclei of the pulvinar-complex do not receive direct retinal innervation (Hayhow, 1958; Singleton and Peele, 1965; Laties and Sprague, 1966; Garey and Powell, 1968). Also

contrary to some suggestions that the LGNd may be a source of visual afferents to the pulvinar-complex (e.g. Rioch, 1931; Vastola, 1961; Altman, 1962; Bruner, 1965), in particular the inferior pulvinar, a recent autoradiographic study (Rosenquist et al, 1974) found no evidence in support of such a pathway, in agreement with an earlier anatomical investigation (Barris et al, 1935).

A retinotopic organization within the inferior pulvinar was demonstrated electrophysiologically by Kinston et al (1969) in addition to the visual field representations in the laminated LGNd and MIN, but these authors found little evidence for retinotopic organization within the medial and lateral pulvinar nuclei from their limited electrode penetrations. The visual field representation was arranged as a mirror-image of that found in the MIN, with the vertical meridian represented along the medial edge and the periphery along the lateral margin adjacent to the MIN.

A later investigation of the receptive field properties of pulvinar-complex neurones also failed to demonstrate any retinotopic organization in the medial and lateral pulvinar nuclei (Godfraind et al, 1972), who concluded that a "random organization" was present in these structures. However the majority of visually responsive cells were sampled in the lateral pulvinar (68%) compared with the medial pulvinar (22%), with an additional bias resulting from only occasional sampling from the dorso-medial portion of the medial pulvinar, judging from their electrode placements (their Fig. 1).

Recent anatomical reports (Graybiel, 1972; Kawamura, 1974; Kawamura et al, 1974) have demonstrated oblique bands of degeneration running downwards in a medio-lateral direction, following cortical or tectal lesions. These consist basically of two separate projection bands

originating from area 17 and superior colliculus (see Fig. 2). Overlapping with the area 17 band is a projection from area 18. Areas 19 and '21' have a double projection; (i) to the medial pulvinar, broadly overlapping the tectal projection band and (ii) to the lateral pulvinar. No projections originating from area '20' appear to terminate in the pulvinar-complex. The Clare Bishop area (CBA) was reported to have similar projections as areas 19 and 21. The results also indicate that the cortical and tectal projection bands may be retinotopically organized, with the upper visual field represented dorso-medially and the lower visual field represented latero-ventrally, the latter lying in the region of the inferior pulvinar, in agreement with the report of Kinston et al (1969).

Visual Areas of the Cortex:

1.4. Visual cortical areas have been classically subdivided on cyto- and myelo-architectonic grounds (Brodmann, 1909) into the primary visual (striate) area of the occipital cortex, designated area 17 of Brodmann, and the secondary visual areas surrounding area 17, which consist of areas 18 and 19 of Brodmann.

The cytoarchitectonically distinguishable areas (17, 18 and 19) in the cat (Otsuka and Hassler, 1962; Sanides and Hoffmann, 1969) contain separate representations of the visual field demonstrable electrophysiologically (Talbot and Marshall, 1941; Hubel and Wiesel, 1962, 1965; Bilge et al, 1967; Tusa, 1974, 1975) and anatomically (Wilson and Cragg, 1967; Garey and Powell, 1967; Niimi and Sprague, 1970).

A fourth visual cortical area was reported by Clare and Bishop (1954) located in the medial wall of the suprasylvian sulcus. This has also

been noted to contain a coarse retinotopic organization (Hubel and Wiesel, 1969; Wright, 1969). A more recent mapping study of this area (Clare Bishop area - CBA) has demonstrated its subdivision into medial and lateral divisions (Palmer et al, 1973 - Fig. 3).

As will be discussed in further detail later, the cytoarchitectonic subdivision of visual cortical areas in primates has been critically challenged by Zeki (1969a, 1974) who proposes a subdivision of secondary visual areas based upon cortico-cortical connectivity patterns, through observations of orthograde degeneration following small cortical lesions. This has revealed that the cytoarchitectonic areas 18 and 19 of Brodmann may be divided into several functionally distinct regions, and has been subsequently confirmed and extended to other species by various authors - see later discussion. The cat (and possibly other members of the Carnivora) appears to be an exception to multiple retinotopic representation in extrastriate cortex in that the secondary visual areas (V II and V III) correspond to the cytoarchitectonic boundaries of areas 18 and 19 of Brodmann.

In a cortico-cortical connectivity pattern study of the cat's visual cortical areas (Heath and Jones, 1972), it has been suggested that there are two additional visual areas in the cat, designated '20' and '21', which show some resemblance to areas 20 and 21 of Brodmann in the temporal cortex of primates. However, Heath and Jones' areas 20 and 21 do not completely correspond to areas 20 and 21 of Brodmann, nor are they entirely compatible with Zeki's observations, but this could be due to differences in lesion size.

Adjacent to area 17 in the medial wall of the cerebral hemisphere an additional representation of the visual field has been electrophysiologically mapped (Kalia and Whitteridge, 1973) which has been termed the 'splenial

visual area' (Fig. 3). This area has been described as resembling limbic cortex in some of its architectonic characteristics and it has been suggested that it is an "integration" area of the cortex (Sanides and Hoffmann, 1969).

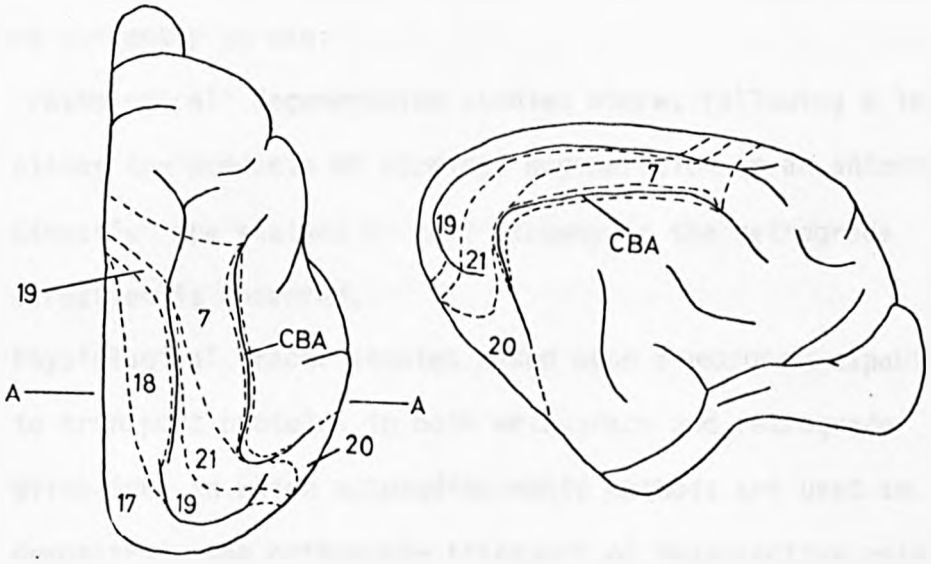
In a recent extensive electrophysiological mapping study of the cat's visual cortex Tusa et al (1975) described single visual field representation - areas 17, 18 and 19; two representations - each of area 20 and 21; and three mirrored representations in each of the medial and lateral divisions of the CBA. They further reported that (i) the extent of the visual field representation in each of these areas differs and (ii) the topographical organization of the visual field represented in these areas differ. Area 17 and the four caudal areas in CBA have first order transformations of the visual field (i.e. adjacent points in the visual field are represented in adjacent cortical foci) while the remaining areas contain second order transformations of the visual field (i.e. adjacent points in the visual field are not represented in adjacent cortical foci) - the second order transforms serving as functional adjuncts to areas containing first order transformations (see Allman and Kaas, 1974a; and 1.7.6.).

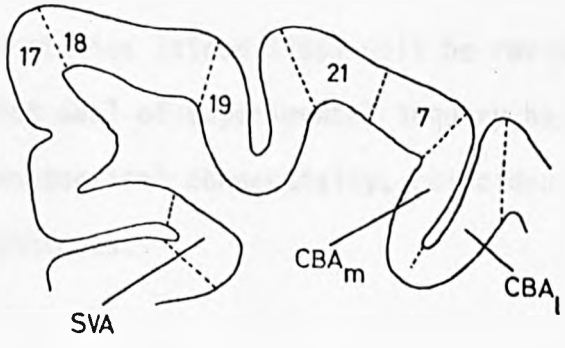
1.4.1. Cortico-cortical connectivity:

In the cat, area 17 has reciprocal connections with areas 18, 19 and CBA, (Wilson, 1968; Shoumura, 1972). The CBA in turn has reciprocal connections with areas 18 and 19, in addition to a projection to limbic cortex in the cingulate gyrus (Shoumura and Itho, 1972).

Area 20 receives an input from area 19 and projects to the amygdala and to area 21. Area 21 in turn projects to the fundus of the posterior syprasylvian sulcus and to the peri-rhinal (limbic) cortex, in addition to

FIG. 3. Dorsal and lateral views of the cat's brain, and a transverse section through A-A outlining the visually associated cortical areas.


19
A
18
17
19
7
CBA
21
20
A
19
21
7
CBA
20


17
18
19
21
7
SVA
CBA m
CBA l

having reciprocal connections with frontal cortex (Heath and Jones, 1970, 1972; Jones, 1974).

Thalamo-cortical Projections:

1.5. Two separate techniques for the investigation of neuroanatomical pathways are currently in use:

(i) 'Pathological' degeneration studies where, following a lesion, either the products of terminal degeneration in an anterograde direction are stained or cell atrophy in the retrograde direction is observed.

(ii) Physiological tracer studies based upon a neurone's capability to transport proteins in both orthograde and retrograde directions in which autoradiographic methods are used to demonstrate the orthograde transport of radio-active amino acids, while the retrograde transport of a tracer protein (e.g. horseradish peroxidase) may be demonstrated by a histochemical reaction.

Only the more recent studies (since 1965) will be reviewed since, during this period, a great deal of experimental inquiry has been devoted to the question of thalamo-cortical connectivity, coincident with improved experimental techniques.

1.5.1. LGNd-complex:

Garey's retrograde studies (Garey, 1965; Garey and Powell, 1967) reported that cell atrophy occurred in the laminated LGNd following lesions in cortical areas 17, 18 and 19, while atrophy in the MIN was only apparent following area 18 and/or 19 lesions. Both the laminated

LGNd and MIN appeared to project to CBA. It was also observed that these projections were retinotopically arranged. It was further noted that atrophy occurred in small and medium sized cells only after area 17 lesions whereas large cell atrophy occurred following lesions in either area 17 or 18.

These observations were supported by a subsequent orthograde degeneration study (Wilson and Cragg, 1967) which, in addition, suggested that the MIN projected to the splenial visual area (also noted in a later study - Sanides and Hoffmann, 1969).

Studies by Glickstein and co-workers (Berkley et al, 1967; Glickstein et al, 1967), while confirming the projection of the laminated LGNd to areas 17 and 18, concluded that the MIN projected principally to area 18.

Niimi and Sprague (1970) reported that laminated LGNd projected to areas 17, 18 and 19 in agreement with previous studies, but suggested that the MIN projected to both areas 18 and 19.

Results from the combined orthograde and retrograde study of Burrows and Hayhow (1970) and a review of earlier investigations suggested to these authors that the laminated LGNd projected to CBA, and that the MIN projected essentially to area 18 alone.

Shoumura (1973) considered that the LGNd comprised two major components: (a) the main laminae (A, A_1 and B), projecting mainly to area 17; and (b) the interlaminar portion (CIN and MIN), projecting to area 18.

The differing conclusions drawn by the authors of these degeneration studies is probably a reflection of differences in definition of the boundaries of visual cortical areas and the pathological consequence of lesions damaging fibres of passage from other structures.

Recent 'physiological' tracer studies which circumvent the

pathological effects of lesion/degeneration methods appear to present a clearer analysis of thalamo-cortical projections. Both autoradiographic (orthograde) and horseradish peroxidase (retrograde) investigations report that laminated LGNd projects to areas 17 and 18, and the MIN to areas 18, 19 and CBA (Rosenquist et al, 1974; Maciewicz, 1974, 1975).

1.5.2. Lateral and posterior thalamic nuclei:

The cortical projections of the pulvinar-complex have been studied using orthograde and retrograde degeneration and, more recently, with autoradiographic and horseradish peroxidase tracer techniques which give essentially similar results. The inferior pulvinar projects primarily to area 19 and the medial division of CBA (Sprague, 1966; Garey and Powell, 1967; Niimi and Sprague, 1970; Burrows and Hayhow, 1970; Niimi et al, 1974; Rosenquist et al, 1974; Kawamura et al, 1975; Maciewicz, 1975). The medial pulvinar is reported to project to areas 19, 20, the splenial visual area (cf. 1.4.1 where MIN was implicated in some degeneration studies), and to both the medial and lateral divisions of CBA (Heath and Jones, 1972; Graybiel, 1972; Kawamura et al, 1974, Kawamura et al, 1975; Niimi et al, 1974; Rosenquist et al, 1974; Maciewicz, 1975). The projections of the lateral pulvinar are essentially to areas 21 and 7 (Heath and Jones, 1972; Graybiel, 1972; Kawamura et al, 1974, 1975; Niimi et al, 1974).

Less experimental effort to date appears to have been devoted to the cortical projections from the dorsal lateral and posterior lateral nuclei, these being areas 5, 7, 19 and 21 (Niimi and Inoshita, 1971; Graybiel, 1973).

Visual Neurophysiology in the Cat

1.6. Current neurophysiological inquiry into the mechanism by which the nervous system processes information from the visual environment is based largely upon studies of the receptive field properties of single cells recorded at sub-cortical and cortical levels in the visual system. The concept of a cell's 'receptive field' was introduced by Hartline (1938) who defined it as "the region of retina which must be illuminated in order to obtain a response in any given fibre" during his investigation of visual response in the frog's optic tract. Many authors now include in their definition all regions which influence a unit's response.

1.6.1. Laminated LGNd:

Receptive field organization: Hubel and Wiesel (1961) noted the similarity between the receptive field organization of laminated LGNd cells and that described by Kuffler (1952, 1953) for retinal ganglion cells. This organization comprised a concentric arrangement with antagonistic on-centre off-surround, or off-centre on-surround regions. The authors found no evidence to suggest that LGN cells exhibited specialized trigger features, e.g. directional selectivity; however, they (and Daniel et al, 1962) noted that cells recorded from lamina B (layer C) had large receptive field centres and appeared to have more sluggish responses of longer latency than cells in laminae A or A_1. Studies using moving stimulus patterns (Kozak et al, 1965; Dreher and Sanderson, 1973) have also revealed this centre-surround organization, and additionally reported a small proportion of binocularly activated and direction selective cells.

Singer and Creutzfeldt (1970), in their quasi-intracellular study of the LGNd, provided evidence of retino-geniculate convergence in which the receptive field centre of a geniculate cell receives its input from one or several retinal ganglion cells of similar type and the geniculate surround from retinal fibres of opposite type. Support for this notion comes from some elegant experiments involving simultaneous recording from both laminated LGNd and retinal ganglion cells which are functionally connected (Cleland et al, 1971a, b). Other evidence suggesting that geniculate centres and surrounds reflect retinal receptive field centre properties derives from the cut-off frequencies for sinusoidally modulated light and the presence of a functional geniculate surround in total dark adaptation (Maffei and Fiorentini, 1971, 1972); and the demonstration of an additional annular zone, the 'outer surround' (Maffei and Fiorentini, 1972; Hammond, 1972a), which is synergistic with the receptive field centre (Hammond, 1972a, b; 1973). The outer surround was also claimed by Ikeda and Wright (1972a, b) to be present in retinal ganglion cells, although weaker than that present in the LGNd.

A property common to both retinal and geniculate levels, the 'periphery effect' was described by McIlwain (1964, 1965) and has recently been further investigated and re-named the 'shift effect' (Fischer, 1974, 1975). In this phenomenon, movement of a pattern in an area remote from the cell's receptive field centre results in a change in the centre sensitivity of the cell, which can be either excitatory or inhibitory for geniculate cells. Independent of the periphery effect, Cleland and co-workers (1971b; 1972) have demonstrated a 'suppressive field' extending outside of the annular surround at both retinal and geniculate levels. Any flashing or moving pattern within this suppressive field inhibited the centre response of the cell.

Occasionally, binocularly activated cells have been recorded in the interlaminar region (CIN) of the laminated LGNd (Bishop et al, 1962), in agreement with the histological observation of binocular retinal overlap (Hayhow, 1958). The results of Suzuki and Kato's (1966) intracellular study suggested the existence of inhibitory influences from the non-dominant eye and that such binocular interaction was present in 75% of cells in the main laminae. Sanderson and colleagues (1969; 1971) later described binocular receptive fields in approximately 80% of laminated LGNd cells, the majority of which had inhibitory fields for the non-dominant eye (also independently reported by Singer, 1970). This inhibitory field may be between 1.5°-6.0° in diameter, a contrast change anywhere within the receptive field being an effective stimulus. Sanderson also provided evidence suggesting that this inhibition is probably an intrageniculate mechanism. Noda et al (1972), in the unanaesthetised cat, classified eight cell types according to their response pattern to moving stimuli. Various types of binocular interaction (inhibition, occlusion, summation and facilitation) were found in 45% of cells in the laminated LGNd. Binocularly driven cells tended to be located dorsally in layer A (possibly including the peri-geniculate nucleus) and in the interlaminar region between layers A_1 and C; in agreement with others (Sanderson et al, 1971), cells with inhibitory fields in the non-dominant eye were found within individual layers.

Sustained (X)/transient (Y) classification: Enroth-Cugell and Robson (1966) further classified retinal ganglion cells in terms of their spatial summation properties. Summation over the receptive field (including both the centre and surround) was found to be either approximately linear (X cells) or non-linear (Y cells). X cells also

tended to have smaller receptive field centres, which were commonly found in the central visual field. These authors further noted that Y cells exhibited an elevated mean discharge to drifting gratings.

Independently, Fukada's and Levick's laboratories reported that retinal ganglion cells could be classified as either Type II or 'sustained', or Type I or 'transient' types (Saito and Fukada, 1970; Fukada, 1971a, b; Cleland et al, 1971b). These classifications refer to the cells' response to a standing contrast at the receptive field centre and to other stimulus conditions, including grating patterns of various spatial/temporal frequencies, receptive field centre size, velocity selectivity to moving targets, the presence or absence of the periphery effect, and the antidromic conduction velocity of retinal ganglion cell axons (see chapter 3 for full description). These observations have been confirmed by other authors (Hamasaki et al, 1973; Hammond, 1972b; Ikeda and Wright, 1972c).

Cleland et al (1971b) and Fukada and Saito (1972) further demonstrated that the sustained/transient, Type II/Type I classification could be extended to cells in the laminated LGNd and that the pathways carrying such information remain separate from retina through to geniculate. These observations have been extended by others (Hammond, 1972b; Hoffmann et al, 1972; Dreher and Sanderson, 1973; Baker et al, 1969). There have been many reports of LGNd cells having mixed properties, receiving both slow (sustained) and fast (transient) retinal input (Cleland et al, 1971b; Hoffmann et al, 1972); Singer and Bedworth (1973) suggested that there was an inhibitory convergence of the sustained and transient system in the LGNd and confirmed previous studies showing convergence of several optic tract fibres onto single sustained or transient LGNd cells (Singer and Creutzfeldt, 1970; Cleland et al,

1971b), although one retinal fibre appeared to provide the dominant input.

In the alert cat, Noda has classified three types of cells (S, T and M) at retinal and geniculate levels (Noda and Adey, 1974a; Noda, 1975). With a stationary patterned field, S-cells showed sustained discharges related to the direction of gaze and to local differences in luminance; T-cells responded transiently to rapid shifts of the retinal image during saccades; while M-cells showed mixed responses. Tested with a moving grating, S-cells discharged to each stripe of the grating, while T- and M-cells responded similarly to S-cells for slow grating motion and with a non-specific elevation in discharge to faster grating motion. S-cells responded in a sustained fashion at either on or off to a diffuse flash, whereas T- and M-cells responded only transiently. Noda (1975) has equated S-cells with sustained cells and T-cells with transient cells as described in acute experiments. M-cells possessed intermediate properties but Noda did not equate them with the mixed property cells of other authors (Cleland et al, 1971b; Hoffmann et al, 1972; Singer and Bedworth, 1973), for the M-cells (recorded in the LGNd) responded with only a single spike to optic chiasm stimulation, with a latency generally intermediate between that of S- and T-cells. The evidence presented in these studies (and that of acute work) suggests that S-, T- and M-cells may alternatively be viewed as forming a continuum of cell types rather than discrete populations.

Many authors (Cleland et al, 1971b; Cleland and Levick, 1974a, b) appear to have assumed a correspondence of the sustained/transient classification with the X/Y classification of Enroth-Cugell and Robson (1966), whereas others have adopted the X/Y classification while using differing diagnostic criteria (Hoffmann et al, 1972; Stone and Fukuda,

1974). In fact, Stone and co-workers have discovered a third class of cells, W cells (see later discussion), which with the X and Y cells form a series (W, X, Y) which strictly reflects the axonal conduction velocities of the three cell types (Stone and Hoffmann, 1972; Stone and Fukuda, 1974). However, recently, Shapley and Hochstein (1975) have reported that, at least for LGNd cells, the time course of the response of a cell (i.e. whether sustained or transient) is not necessarily correlated with its spatial summation properties (X or Y). Ikeda and Wright (1976) have also reported the existence of transient-X cells in the laminated LGNd, in addition to sustained-X and transient-Y types.

The more recently discovered third class of retinal ganglion cells (W cells) (Stone and Hoffmann, 1972), had very slowly conducting axons and lacked the classical centre-surround receptive field organization (classified as 'suppressed-by-contrast' or direction-selective/unselective 'excited-by-contrast' types). In a subsequent report, Stone and Fukuda (1974) provided a comprehensive description of W cells which included centre-surround types (58%), phasic on-off centre types (34%), direction-selective and suppressed-by-contrast types (9%). The concentric W-cells were further classified as either phasic or tonic, according to their response to standing contrast. Independently, Cleland and Levick (1974a) sub-divided sustained and transient cells into 'brisk' and 'sluggish' types, the 'brisk' sustained and 'brisk' transient types probably corresponding to the X and Y classification respectively of Enroth-Cugell and Robson (1966). They also described some rare types - local edge detectors, direction-selective cells, colour-coded cells, uniformity detectors, and edge inhibitory off-centre cells which, together with 'sluggish' sustained and 'sluggish' transient cells, probably correspond to Stone's W cells (Cleland and Levick, 1974b). Both

Cleland and Levick (1974a, 1974b) and Stone and Fukuda (1974) have related the functional classification of retinal ganglion cells to the morphological classification of Boycott and Wassle (1974), who describe three basic cell types (, β and γ cells), probably corresponding to the Y, X and W classification respectively of Stone and Fukuda, and the brisk-transient, brisk-sustained, and sluggish together with rare cell types respectively of Cleland and Levick).

1.6.2. MIN:

The bulk of electrophysiology on the MIN has been primarily concerned with mapping its visual field representation (Seneviratne and Whitteridge, 1962; Bishop, 1965; Kinston et al, 1969; Sanderson, 1971). These authors noted the resemblance between centre-surround receptive fields of cells in the MIN and laminated LGNd particularly those in layer C. In either case the nasotemporal overlap was more than 2° (compared with less than 2° for A laminae cells) and receptive field centres were larger than in the A laminae.

Although histological studies (Hayhow, 1958) have indicated a large binocular overlap of retinal afferents in the MIN, electrophysiological studies have only reported binocularly-activated cells in similar proportions as found in the laminated LGNd.

1.6.3. Pulvinar-complex:

Since early reports of visually evoked potentials in the cat's pulvinar-complex (Buser et al, 1959), others have reported visually responsive cells (Koenig and Frazier, 1969; Huang and Lindsley, 1973), although few receptive field studies have been published. Suzuki and Kato (1969) described cells with large, uniform receptive fields which

yielded on-off responses to flash and that visual responsiveness was highly dependent on reticular activity. Kinston et al (1969) commented that cells recorded in the pulvinar nuclei were difficult to activate and that their receptive fields were difficult to define. Some cells in the inferior pulvinar were reported to have concentric centre-surround organization similar to that described by Kuffler (1953), while other cells (including those in the medial and lateral pulvinar nuclei) had binocularly-activated fields or were direction-selective in their response to moving stimuli and generally had larger receptive fields than geniculate cells.

Wright (1971) found that 60% of medial and lateral pulvinar cells were visually influenced and defined three groups:

(i) diffuse on-off fields (20-90° diameter);

(ii) concentric centre-surround fields (1-10° diameter) responding phasically; and

(iii) discontinuous-movement sensitive cells (6-90° diameter fields) responsive to small rapid movements, with a variety of preferences for stimulus size, directionality and orientation.

Specialized receptive field properties were also reported by Godfraind et al (1972) who classified cells with (i) diffuse receptive fields and (ii) restricted receptive fields, the latter group exhibiting orientational, movement and directional properties.

1.6.4. Visual Cortex:

A series of studies by Hubel and Wiesel (1959, 1962, 1963, 1965) has provided both the initial and perhaps the most fundamental contribution to the knowledge of cortical receptive fields. These authors described three basic types of cells ('simple', 'complex' and

'hypercomplex') which can be distinguished from afferent fibres from the LGNd in that most can be driven by either eye and are sensitive to the orientation of flashed or moving bar or edge stimuli.

Simple cells have separate 'on' and 'off' regions within their receptive fields, arranged in parallel strips, which can be mapped with flashed spots or bars. They are further distinguishable in showing spatial summation within and antagonism between the 'on' and 'off' regions. The optimal moving stimulus can be predicted from the spatial organization of the 'on' and 'off' regions. However, contrary to Hubel and Wiesel (1962), Bishop et al (1974) have reported that directional preference can not be predicted from the static receptive field map. Furthermore, the dynamic receptive field map derived with moving stimuli consists of a central excitatory zone flanked by one or two inhibitory side bands (Henry and Bishop, 1971) does not correlate with the static receptive field map (Bishop et al, 1972). According to Hubel and Wiesel, simple cells appear to be restricted to area 17; however, more recently, simple cells have also been recorded in area 18 (Tretter et al, 1975; Singer et al, 1975a ; P. Hammond, personal communication).

Complex cells resemble simple cells in being responsive to moving stimuli and in showing selectivity for direction or orientation. They may be distinguished by their larger receptive fields (more than 3°), and in being less selective for stimulus position within the receptive field. Only rarely are their fields divisible into antagonistic 'on' and 'off' areas with flashed stimuli, and within these there is no spatial summation; other complex cells, if they are responsive to flash, yield 'on-off' discharges throughout their receptive fields.

Two subtypes of hypercomplex cells may be recognized; 'lower-order'

(found in areas 17, 18, 19 and the medial division of the Clare-Bishop area (CBA)) and 'higher-order' (found only in area 19). The lower-order types, in addition to being selective for orientation, are also selective for stimulus length as a consequence of one or two end-inhibitory zones. Lower-order hypercomplex cells have recently been subdivided into Type 1 (simple) and Type 11 (complex) fields, distinguished by their simple- or complex-cell type responses to movement (Dreher, 1972; Rose and Blakemore, 1974; Rose, 1974). Rose (1974) has claimed that Type 1 (simple) and Type 11 (complex) lower-order hypercomplex cells constitute the extremes of a continuum for simple and complex cells respectively. Higher-order hypercomplex cells are yet more selective in that an optimally 'end-stopped' light/dark bar may elicit a response to movement in either of two directions oriented at right angles to each other. To date, only Hubel and Wiesel's 1965 study provides analyses of these higher-order types.

Pettigrew and co-workers (1968a) classified cells as simple or complex, using differing criteria from those of Hubel and Wiesel. They reported that simple cells were rarely driven by flashed stimuli. Simple cells were distinguished by their preference for slow velocities of movement, low spontaneous firing rate and crisp response to moving stimuli (as visualized from average response histograms), whereas complex cells had brisk spontaneous firing, a preference for faster velocities (more than $15°.sec^{-1}$) and, compared with simple cells, broad and irregular average response histograms.

Hubel and Wiesel (1962) also noted that simple cells were commonly located in or near layer IV (a region with predominantly stellate cells), while complex and hypercomplex cells were more often found in the more superficial and deeper layers (predominantly pyramidal cells). Hubel and

Wiesel proposed a hierarchical or serial organization, with simple cells receiving the bulk of their input from the LGNd and subsequently providing the predominant drive for complex cells, in addition imposing similar orientation preferences, a possible explanation of the columnar organization (see later discussion). This model has received recent support from the elegant intracellular studies which showed that the majority of simple cells are stellate and virtually all complex cells are pyramidal (Van Essen and Kelly, 1973; Kelly and Van Essen, 1974).

An alternative theory of parallel processing of visual information, by the sustained (slow) and transient (fast) pathways has been proposed by Stone (1972). This derives from Stone and Hoffmann's (1971) demonstration that slow and fast geniculo-cortical afferents activate, monosynaptically, simple and complex cells respectively in area 17. These observations were extended in a later report (Stone and Dreher, 1973) which compared the responses of geniculate sustained and transient cells (characterized according to their afferent conduction velocities) and subsequently with those of simple and complex cortical cells. Stone and Dreher also noted that sustained cells (presumed to be large) projected to areas 17 and 18, in apparent agreement with anatomical reports (Garey and Powell, 1967; Rossignal and Collonnier, 1971) that large axons bifurcate to areas 17 and 18 and small axons project only to area 17.

Studies from other laboratories provide further evidence in support of parallel processing of visual information. Movshon (1975) investigated the velocity tuning of simple and complex cells, and reported that simple cells preferred lower velocities (mean $2.2°.sec^{-1}$) than complex cells (mean $18.8°.sec^{-1}$); simple cells responded poorly at velocities higher than $20°.sec^{-1}$ whereas complex cells still discharged

briskly. This is difficult to reconcile with the idea that simple cells provide the main drive to complex cells. Maffei and Fiorentini (1973) and Movshon and Tolhurst (1975) claimed that simple cells resembled sustained cells whereas complex cells resembled transient cells in their sensitivity to moving sinusoid and square wave gratings, further supporting a model of parallel processing. Recent reports from this laboratory (Hammond and MacKay, 1975a,b, 1976) have demonstrated that simple and complex cells are differentially sensitive to motion of textured 'visual noise', observations which are again inconsistent with serial processing.

Ikeda and Wright (1974, 1975a,b) have demonstrated 'sustained' and 'transient' cortical cells in area 17, based upon the temporal response to an optimally oriented stationary contrast at the receptive field centre and on spatial/temporal frequency sensitivities to gratings. This classification of cortical cells appears to be independent of Hubel and Wiesel's simple/complex classification. Ikeda and Wright suggested that, functionally, this parallel organization provides a high spatial resolving channel (sustained cells) and a high temporal resolving channel (transient cells) from retina through to cortex. Although their results appear contrary to Stone's suggestion that the sustained system is associated with simple cells and the transient system with complex cells, Stone and Dreher's (1974) results are consistent with Ikeda and Wright's; for Stone and Dreher found cortical cells with separate 'on' and 'off' receptive field areas (presumed simple) and 'on-off' receptive fields (presumed complex) receiving a slow afferent input. Singer and co-workers (1975a,), in comparing the receptive field characteristics of cells in areas 17 and 18 with their afferent and efferent connections, reported that simple and complex cells

(in area 17) can be driven monosynaptically by either slow (sustained) or fast (transient) afferents, whereas cells in area 18 (some resembling simple cells) are driven only by fast (transient) afferents. Other laboratories have reported sustained and transient cortical cells (using the standing contrast criterion), independent of the simple/complex classification (D.P. Andrews and P. Hammond, personal communication; Kelly and Van Essen, 1974; Movhson, 1975), in support of Ikeda and Wright's observations. Movshon further commented that sustained-simple cells tended to prefer slower rates of movement than transient-simple cells; he also claimed only to have found transient-complex cells.

Many authors (Maffei and Fiorentini, 1973; Ikeda and Wright, 1974; Movshon and Tolhurst, 1975) have identified the modulated or unmodulated types of response to a moving grating, initially described by Campbell et al (1969), as characteristic of simple and complex cells respectively. Both Maffei and Fiorentini, and Movshon and Tolhurst, suggest this to be evidence of drive from X and Y cells (as defined by their modulated or unmodulated responses - Enroth-Cugell and Robson, 1966), whereas Ikeda and Wright claim that the modulated/unmodulated responses shown by simple and complex cells are independent of their sustained and transient characteristics. This discrepancy may be accounted for by non-equivalence between sustained and transient cells at cortical levels compared with those at lower levels, or by the recent report that the sustained/transient classification does not necessarily equate with the X/Y classification (Shapley and Hochstein, 1975).

Columnar organization: A columnar arrangement of cells extending radially from the white matter to the cortical surface which appeared to process the input from one receptor population (cutaneous and deep

tissue receptors) was discovered by Mountcastle (1957) in somatosensory cortex. This was followed by reports of a similar organization in visual cortex (Hubel and Wiesel, 1962, 1963) in which cells with similar preferred orientations and receptive field location were arranged in columns. These columns were irregular in cross-section (0.1-0.5mm diameter) and adjacent columns contained different preferred orientations. Hubel and Wiesel also provided evidence for ocular dominance columns in cat (Hubel and Wiesel, 1962, 1965b) and later, more convincingly, in monkey (Hubel and Wiesel, 1968, 1972). More recently, Hubel and Wiesel (1974a, 1974b) in both the macaque monkey and the cat (although only based on four penetrations for the cat) reported a highly ordered arrangement of orientation and ocular dominance columns and introduced the term 'hypercolumn' which refers to a group of columns containing either a complete orientation representation (180°) or a left-plus-right ocular dominance set. Albus (1975b) provides evidence of continuous representation of orientations in the cat striate cortex (using a much larger sample) in which all orientations are repeated within a cortical cylinder termed an 'orientation subunit' (approximately 600mμ diameter). Albus has further suggested (1975a) that cells representing a given area of the visual field are distributed within a cylinder of cortex (2.6-2.8mm diameter) which constitutes a 'spatial subunit'. The extent of the visual field representation within these spatial subunits varies with eccentricity (e.g. 0.7° at the area centralis, increasing to 2.6° at 6-10° from the area centralis). Multiple orientation subunits are present in each spatial subunit, and since spatial subunits are of similar size it implies that the number of orientations analyzed per unit area of the visual field for central vision will exceed that in the more peripheral visual field.

Binocularity: The majority of cat cortical cells are binocularly influenced (Hubel and Wiesel, 1962, 1965; Pettigrew et al, 1968, Henry et al, 1969; Noda et al, 1971a,b). For a minority of cells the influence from one eye may be inhibitory or only provide subliminal excitation, but most can be driven by both eyes.

It has been suggested that the neurophysiological basis for depth discrimination in area 17 may be due to:

(i) cells with receptive fields in the two retinae that are not in correspondence, i.e. that show retinal disparities, the optimal disparity varying from cell to cell (Barlow et al, 1967; Nikara et al, 1968; Pettigrew et al, 1968; Blakemore, 1970; Blakemore and Pettigrew, 1970); and

(ii) cells with preferred orientations that are different for the two eyes (Blakemore et al, 1972).

Blakemore (1970) in addition reported a columnar organization of disparity-sensitive cells: 'constant depth' columns (which contain cells with similar disparities) and 'constant direction' columns (containing cells in which the receptive fields of the contralateral eye are superimposed). However, Blakemore's criteria for identifying a column were based only on small cell samples (2-5 cells) recorded within a distance of 2mm, and histological controls were lacking.

Hubel and Wiesel (1973) reported that, for almost all cells in area 17 of the cat, the retinal disparity was negligible and suggested that such cells only occur in extrastriate cortex (where disparity-sensitive cells have been reported in the cat - Pettigrew, 1972, 1973), as in the monkey (Hubel and Wiesel, 1970), and also as more recently found in sheep V II (Clarke and Whitteridge, 1973; Clarke et al, 1976). Hubel and Wiesel (1970) observed that 'binocular depth cells' recorded

from macaque area 18 occurred in clusters (suggestive of a columnar organization) and Clarke and colleagues were able to demonstrate 'constant disparity' columns in sheep V II. Therefore it is probable that a columnar organization of disparity-sensitive cells is present in the cat and that these may reside in area 18 - Blakemore (1970) used no histological controls and it is possible that he was actually recording from area 18.

Clare-Bishop area (CBA): All electrophysiological studies of receptive field properties of this visual area have been primarily concerned with the medial division of CBA (Hubel and Wiesel, 1969; Wright, 1969; Spear and Baumann, 1975a; Camarda and Rizzolatti, 1976). Hubel and Wiesel (1969) described only complex and lower-order hypercomplex cells, most of which could be driven by either eye, and which generally had larger receptive fields than those recorded in areas 17, 18 or 19. Often, the receptive fields occupied most of a visual quadrant and extended into the ipsilateral visual field for several degrees. They also claimed that cells responded optimally to moving, appropriately oriented bars and showed direction selectivity. Wright (1969) confirmed these observations and, in addition, described 'movement-sensitive' cells showing little orientation, direction or length specificity. Both of these studies were restricted to the 'middle' visual representation of the medial division of CBA.

More recent studies (Spear and Baumann, 1975a; Camarda and Rizzolatti, 1976) have confirmed and extended the previous studies. Spear and Baumann classified cells as 'direction selective' (81%), some of which showed spatial summation within the receptive field and/or inhibitory surrounds; 'movement sensitive' (7.5%), responding to movement in any direction; 'stationary' (5%), with concentrically organized

receptive fields; and 'diffuse' (6.5%). Contrary to previous reports (Hubel and Wiesel, 1969; Wright, 1969), Spear and Baumann concluded that most cells were not sensitive to changes of orientation. They further investigated the medial division of CBA throughout its anterior-posterior extent (including the rostral, middle and caudal visual representation areas) and found no apparent differences in receptive field properties, although the extent of visual field representation in each area varied in accordance with previous mapping studies (Palmer et al, 1973; Tusa et al, 1975). Camarda and Rizzolatti (1976) reported recordings from a few cells in the lateral division of CBA; such cells were binocularly driven, possessed large receptive fields and were directionally selective.

The effect of unilateral and bilateral ablations of areas 17, 18 and 19 on the response properties of cells in the CBA results in a loss of directional specificity and a reduction of binocularly driven cells, while a variety of receptive field properties are not affected, e.g. responsiveness to small stimuli, presence of spatial summation and the incidence of surround inhibition - properties presumably derived from the thalamic afferent input (Hubel and Wiesel, 1969; Spear and Baumann, 1975b).

Anterior middle suprasylvian gyrus (AMSS): This visually responsive area corresponds to area 7 (and possibly part of area 21) and receptive field properties have been described by various authors (Dubner and Brown, 1968; Dow and Dubner, 1969, 1971; Straschill and Schick, 1974). All the receptive fields are large (more than 15° across): S-cells respond only in an 'on-off' fashion to flashed stimuli; while M-cells (either small- or large-field types) respond only to moving stimuli, often showing direction selectivity. Ablation of areas 17 and 18 results

in a loss of visual responsiveness, whereas superior collicular ablation has little, if any, apparent effect (Dow and Dubner, 1971). Pre- and post-saccadic responsive cell types have been described in awake cats, which has led to suggestions that this area is involved with visual attention and orientation (Dow and Dubner, 1971; Straschill and Schick, 1974).

Comparative Aspects:

1.7. In order to appreciate the significance of a particular substructure within the central nervous system it is of value to compare the organization found in cat with other species. Therefore, a description of the comparative aspects of organization within the visual thalamus (comprising the dorsal and ventral divisions of the LGN, and the pulvinar complex) and visual cortex will be outlined:

1.7.1. LGNv:

The differentiation of this division of the LGN in mammals is very varied. Where best differentiated, e.g. in the ungulates and carnivores, it is composed of an internal and an external division. The internal division may be further subdivided into a pars dorsalis and a pars ventralis and the external division into internal and external sub-layers (Niimi et al, 1963). Differentiation of the LGNv into internal and external divisions has in fact been described for most mammals so far investigated (Clark, 1929; Hayhow, 1967; Campbell, 1972), although the subdivisions have been less frequently described.

Two patterns of retinal input to the LGNv may be seen:

(i) a contralateral projection to the entire external division,

but only partial ipsilateral input, as seen in the rat, hedgehog and marsupials (Campbell, 1972);

(ii) ipsilateral and contralateral projections spread throughout the external division, as seen in the tree shrew and squirrel monkey (Campbell, 1972).

Retinal input to the internal division has not been demonstrated. However, most studies have employed limited post-operative periods and evidence is accumulating that short survival times (less than 5 days) are important as some pathways show rapid degeneration and debris clearance within the 7-10 day survival times commonly used.

An ipsilateral projection from the superior colliculus to the LGNv has also been described for a variety of species (Abplanalp, 1970; Benevento and Ebner, 1970; Myers, 1963).

Similarly, retinotopically organized projections from visual cortex are well documented and terminate in both internal and external divisions of LGNv (Abplanalp, 1970; Harting and Noback, 1971; Meikle and Sprague, 1964).

1.7.2. LGNd:

In a comparative study, Campbell (1972) has provided the following classification of the LGNd according to cytoarchitecture and the degree and pattern of segregation of ipsilateral and contralateral inputs (the extent of which reflects the degree of binocular overlap exhibited by a given species), which appears to hold good for other species described subsequently or not included in Campbell study:

(A) No cytoarchitectural laminae present:

(i) a contralateral retinal projection terminating diffusely throughout the nucleus; while an ipsilateral projection,

if present, is localized to a portion of the nucleus overlapping the contralateral projection field (e.g. opossum and cetacea (e.g. bottlenose dolphin) - Lent et al, 1976; Jacobs et al, 1975);

(ii) a contralateral retinal projection throughout the nucleus except for a few localised areas where ipsilateral input terminates (e.g. rat, hedgehog, squirrel and ungulates - Hall and Ebner, 1970; Tigges, 1970; Karamanlidis and Magras, 1972, 1974; Lund et al, 1975);

(B) Cytoarchitecturally definable layers:

(i) partial lamination, coupled with an undifferentiated mass of cells containing concealed lamination which can only be revealed by histological methods (e.g. owl, monkey, squirrel monkey and carnivores - Jones, 1966; Wong-Riley, 1972; Sanderson, 1974);

(ii) complete lamination (no concealed lamination), where there may be (a) no overlap of contralateral and ipsilateral projection fields (e.g. slow loris, bush baby, gibbons, rhesus monkey, chimpanzee and man (Goldby, 1957; Heiner, 1960; Hassler, 1966; Kanagasuntheram et al, 1969; Campos-Ortega and Hayhow, 1970; Kaas et al, 1972a; Guillery et al, 1975; Glendenning et al, 1976)), or (b) overlapping contralateral and ipsilateral projection fields (e.g. tree shrew and marsupial phalanger - Campbell et al, 1967; Hayhow, 1967).

An additional cell layer (layer 'O' or 'S') has been described sandwiched between the ventral magnocellular layer and the optic tract in

both primates (Prosimians, New World and Old World monkeys) and sub-primates, receiving ipsi- and contralateral retinal innervation Giolli and Tigges, 1970; Campos-Ortega and Hayhow, 1970; Kaas et al, 1972, 1976). This layer may be homologous to the ventral, parvocellular, layer described in carnivores (Guillery, 1970; Sanderson, 1974).

As Campbell (1972) has noted, lamination in the LGNd appears to be found in those mammals specialized for flight, gliding, and rapid locomotion in their aboreal or terrestrial habitat - "The rapid evaluation of spatial relations, including depth perception, is seemingly a common functional challenge in those groups of animals possessing highly organized LGNd and it is hard to avoid the notion that lamination is involved."

Geniculo-cortical projections: Many authors have considered that the geniculo-cortical projection to areas 17, 18 and possibly 19 in the cat are peculiar to this species, whereas in other species e.g. primates (Wilson and Cragg, 1967; Wiesel et al, 1974; Glendenning et al, 1976) and rodents (Rose and Malis, 1965; Valverde and Esteban, 1968; Ribak and Peters, 1975) the LGNd projects exclusively to area 17. Ebbesson (1972), in a comparative review of the vertebrate visual system, outlined the interspecies variations found in thalamo-cortical projections. At one extreme (e.g. the cat) the LGNd projects to areas 17 and 18, and the pulvinar-complex only to extrastriate cortex, whereas at the other extreme, e.g. for the opossum (Benevento and Ebner, 1971a; Coleman and Winer, 1976), the LGNd projects to only area 17 and the pulvinar-complex to both striate and extrastriate cortex. In yet other species, e.g. the tree shrew, mouse, rat and primates, no overlap of projection is apparent, with the LGNd projecting only to striate cortex and the pulvinar-complex only to extrastriate cortex.

More recent studies using the newly-developed, sensitive tracer techniques suggest there is perhaps less diversity than indicated from the results of earlier degeneration methods. HRP studies in the squirrel monkey (Wong-Riley, 1976), with injection sites in area 18, showed projections from medium and large cells in both the parvocellular and magnocellular layers in the LGNd, bearing some resemblance to the organization found in the cat. These injections were, however, made in a restricted portion of area 18 on the dorsal surface of the occipital lobe and there remains the question of whether this projection is a generalized or specific one?

1.7.3 Extrageniculate retinal projection fields:

In addition to retinal projections to the dorsal and ventral divisions of the lateral geniculate nucleus there are other retinal projection fields in the visual thalamus (excluding the accessory optic tract and pretectal nuclei).

Carnivora: Organization within the thalamus of the domestic cat appears to be representative of its order, according to Rioch's (1929) and Sanderson's (1974) studies of a variety of carnivore species, with a bilaterally innervated MIN readily distinguishable.

Ungulata: Species investigated include the pig, ox, sheep, goat and horse (Campos-Ortega, 1970; Cummings and De Lahunta, 1969; Karamanlidis and Magras, 1972, 1974; Nichtherlein and Goldby, 1944; Rose, 1942). Most of these authors have identified a bilateral projection field lying between the 'laminated' LGNd and pulvinar, initially described in the sheep as the pars geniculata pulvinaris (Rose, 1942). This projection field is composed of large cells with a poorly defined vertical lamination, and recent authors

(Cummings and De Lahunta, 1969; Campos-Ortega, 1970; Karamanlidis and Magras, 1972, 1974) regard it to be homologous with the feline MIN.

Rodentia: The rabbit and rat are the experimental representatives of this order; however, for neither species is there a description of an extrageniculate retinal projection (Giolli and Crothrie, 1969; Hayhow et al, 1962; Lund et al, 1975; Hickey and Spear, 1976). Electrophysiological mapping studies have, however, revealed secondary representations of the visual field in the posteromedial portion of the LGNd in rabbit (Choudhury and Whitteridge, 1965) and in the anteromedial margin of rat LGNd (Montero et al, 1968). Within the rat's LGNd Lund and co-workers (1975) suggested a small band on the medial border may possibly be a 'separate nucleus' comparable to the feline MIN. These authors also described an additional bilateral retinal projection field wedged in between the LGNd and LGNv, and referred to as the 'intergeniculate leaflet' in an autoradiographic study (Hickey and Spear, 1976).

Primatia: Species constituting this order may be further classified as either (i) Prosimian, (ii) New World or (iii) Old World primates. (In primates the LGNv is found dorsal to the LGNd and referred to as the peri-geniculate nucleus - PGN.)

(i) For two representative Prosimian species, the tree shrew and bush-baby, no extrageniculate retinal projections have been reported (Campbell et al, 1967; Tigges and Tigges, 1970).

(ii) Three New World species have been extensively studied, the marmoset, owl and squirrel monkey. It is only since the advent of autoradiographic techniques in neuroanatomy that a bi-lateral retinal input to a cell group located

medial to LGNd in the squirrel monkey has been demonstrated (Tigges and O'Steen, 1974). This projection field is represented by a ventral extension of the PGN (probably equivalent to the parageniculate nucleus of Polyak, 1957).

(iii) In Old World species, Campos-Ortega and Hayhow (1971) have described a bi-lateral projection field situated between the PGN and LGNd in rhesus monkey and baboon. This projection field was initially reported by Minkowski (1920) as the 'intermediäre Zellgruppe' and has since been re-discovered in the rhesus monkey (Polyak, 1957; Hendrickson et al, 1970) and the gibbon (Kanagasuntheram et al, 1969).

A separate bilateral retinal projection, restricted to a rostral portion of the inferior pulvinar adjacent to the LGNd, has been described in the rhesus monkey and baboon but not found in Prosimian or New World species (Campos-Ortega et al, 1970; Tractenberg, 1974).

1.7.4. Pulvinar-complex:

A major problem in reviewing the organization of the nuclei constituting the lateral and posterior thalamic groups (which includes the pulvinar-complex) from a comparative standpoint is the range of nomenclature used, a factor outlined earlier (1.3.0.). In an attempt to unify classification, Niimi and Kuwahara's (1973) cytoarchitectural description of the mammalian dorsal thalamic nuclei will be followed. The extent of nuclear differentiation within the pulvinar-complex is

variable. In rodents and ungulates there is little differentiation within this structure (referred to by many authors as the lateral posterior or pulvinar nucleus), while inferior, medial and lateral divisions may be differentiated in carnivores and primates. However for some species, e.g. the bush baby and owl monkey (not considered in Niimi and Kawahara's study), other authors have only been able to sub-divide the pulvinar-complex into inferior and superior divisions (Allman and Kaas, 1972; Glendenning et al, 1975). It may be that the superior pulvinar is an undifferentiated form of the lateral and medial pulvinar nuclei, a speculation which future comparative connectivity studies should be able to resolve. This point will, however, be considered further in chapter 7 with regard to the evolution of the pulvinar-complex as exemplified by relevant data from the present study on the cat.

Based on connectivity-pattern studies, Diamond and co-workers (Diamond and Hall, 1969; Harting et al, 1972) have argued that the primate pulvinar-complex may be regarded as comprising 'intrinsic' and 'extrinsic' portions, while in sub-primates only an 'extrinsic' portion is present. The extrinsic portion (comparable with the inferior pulvinar) is defined as that region receiving a projection from the superficial layers of the superior colliculus. The intrinsic portion (equivalent to the lateral and medial pulvinar nuclei) is regarded as that region reciprocally connected with neocortex, particularly the parieto-temporal cortex which parallels the voluminous expansion of the lateral and medial pulvinar, and posterior lateral nuclei as the order Primatia is ascended.

Termination of striate cortical projections within the pulvinar-complex may include both the intrinsic and extrinsic portions. In those species where the pulvinar-complex is not differentiated there may be

either

(i) an overlap of the striate with the tectal projections, e.g. rat (Nauta and Bucher, 1954), rabbit (Giolli and Guthrie, 1971), opossum (Benevento and Ebner, 1970), and hedgehog (Harting et al, 1972), or

(ii) a complete (or near-complete) segregation of striate and tectal afferents as found in the marsupial phalanger (Rockel et al, 1972), squirrel (Robson et al, 1974; Robson et al, 1975), and most mammals where the pulvinar-complex can be differentiated, e.g. the cat (Graybiel, 1972), tree shrew (Abplanalp, 1975), bush baby (Tigges et al, 1973; Glendenning et al, 1975), squirrel monkey (Mathers, 1971, 1972) and rhesus monkey (Benevento and Fallon, 1975; Benevento, 1975; Benevento and Rezak, 1976).

While the projections of the primate inferior and lateral pulvinar nuclei to extrastriate cortex (areas 18, 19, 20 and 21 of Brodmann) are well documented (e.g. Clark and Northfield, 1937; Cragg and Ainsworth, 1969; Mathers, 1972; Lin et al, 1974; Spatz and Erdman, 1974; Glendenning et al, 1975; Ogren and Hendrickson, 1975; Benevento and Rezak, 1976), recent evidence suggests that the tecto- and cortico-recipient zones in the inferior pulvinar may have differentiable cortical projection sites (Glendenning et al, 1975; Rezak and Benevento, 1975a, 1975b; Benevento and Regal, 1976) - a similar situation may also hold for the cat (Kawamura et al 1975; see also chapter 7) and the squirrel (Robson et al, 1974). Further, Benevento and Rezak (1976) have reported that there is a multiple, retinotopically organized, projection from the inferior pulvinar to extrastriate cortex which is in agreement with the recent functional parcellation of extrastriate cortex as reviewed later

(1.7.6.).

The medial pulvinar is reported to project to parieto-temporal cortex (areas 7 and 21), frontal and orbital cortices (Locke, 1960; Mathers, 1972; Trojanowski and Jacobson, 1974; Benevento and Rezak, 1976).

Situated medial to the inferior pulvinar and ventral to the medial pulvinar lies a nuclear region, the posterior or suprageniculate nucleus, which is occasionally included as either the inferior or medial pulvinar. On the basis of its connectivity with the visual system, receiving projections from striate cortex, extrastriate cortex, and the superior-colliculus (Spatz et al, 1970; Mathers, 1971, 1972; Spatz and Tigges, 1973; Spatz and Erdmann, 1974; Hollander, 1974) and projecting to the middle temporal area (MT) (Lin et al, 1974; Spatz, 1975), it should perhaps be regarded as the 'posterior nucleus of the pulvinar complex'.

There is a scarcity of data on the projections of the lateral thalamic nuclear group. The posterior lateral nucleus merges into the medial pulvinar and would appear to have similar projections to parieto-temporal cortical areas (Mathers, 1972; Glendenning et al, 1975).

Projections from the pulvinar-complex to the extrastriate cortex (areas 18, 19 and 'temporal visual areas') have been demonstrated for a number of sub-primate species, e.g. grey squirrel (Kaas et al, 1972b; Robson et al, 1974), hedgehog (Hall and Diamond, 1968) and tree shrew (Harting et al, 1973a). For the squirrel, at least, there is evidence of a differential projection from the rostral portion of the pulvinar-complex (which appears to contain segregated projection zones from the superior colliculus and striate cortex) to areas 18 and 19 and from the caudal portion (containing only a tectal projection zone) to the temporal visual areas (Kaas et al, 1972b; Robson et al, 1974).

In addition to pulvinar projections to extrastriate areas, studies

by Benevento and co-workers have demonstrated extrageniculate projections to layers I and VI of striate cortex (cf. LGNd projection mainly to layer IV) in opossum and rhesus monkey (Benevento and Ebner, 1971; Benevento et al, 1976).

Electrophysiological mapping studies have revealed a retinotopic organization within the inferior pulvinar of the owl monkey and squirrel monkey (Allman et al, 1972; Mathers and Rapisardi, 1973). A similar organization in the inferior pulvinar is also indicated from published data on the rhesus monkey (Kaas et al, 1972a) and tree shrew (Kaas, personal communication in Glendenning et al, 1975). While searching for retinotopic organization in the lateral and medial pulvinar nuclei. Mathers and Rapisardi (1973) noted that somatosensory, but not visuo-somatosensory, cells were apparently somatotopically organized. No reference was made by Stewart et al (1973) to any retinotopic organization in their study of the rabbit's visual thalamus.

1.7.6. Primary visual cortex:

Strictly, the primary visual cortex is that area of cortex where fibres of the optic radiation terminate and is readily characterized in most species by the line of Gennari, hence the term 'striate' cortex. On cytoarchitectonic grounds the primary visual cortex is referred to as 'area 17' (e.g. Brodmann, 1905, 1909).

(Note: In describing cortical visual areas as defined in anatomical connectivity studies, Arabic numerals will be used (e.g. V1); Roman numerals (e.g. V I) will be used for physiologically defined areas).

The striate cortex has been mapped electrophysiologically in a variety of species including both primates (Talbot and Marshall, 1941; Woolsey et al, 1955; Daniel and Whitteridge, 1961; Cowey, 1964; Hubel and

Wiesel, 1968; Allman and Kaas, 1971a; Woolsey, 1971) and sub-primates (Thompson et al, 1950; Adams and Forrester, 1968; Kaas et al, 1970, 1971; Hall et al, 1971; Drager, 1975), the primary cortical representation (V I) being contained within the cytoarchitectonic area 17.

1.7.6. Extrastriate cortex:

The extent to which the extrastriate cortex can be subdivided has been a matter of some dispute and has been extensively reviewed by Zeki (1969a).

Cytoarchitectonic subdivision: Brodmann (1905, 1909) divided the area surrounding the striate cortex into two divisions designated areas 18 and 19, a nomenclature of subsequently widespread adoption. Many authors have, however, been unable to define such cytoarchitectonic boundaries within the primate extrastriate cortex (Lashley and Clark, 1946; von Bonin and Bailey, 1947; Zeki, 1969a; Spatz et al, 1970; Martinez-Millan and Hollander, 1975).

Retinotopic organization: Both anatomical and physiological work since the late 1960's has demonstrated the existence within the primate extrastriate cortex of several anatomically and functionally distinct visual areas.

Investigation of cortico-cortical connectivity in the rhesus monkey, using orthograde degeneration techniques, has revealed a topographic projection from area 17 (V1) to two areas in extrastriate cortex (V2 and V3), in which area V2 mirrors V1 and area V3 mirrors V2 (Cragg and Ainsworth, 1969; Zeki, 1969b; Cowey, 1971, 1973). There is also a third projection to the posterior bank of the superior temporal sulcus (V6), which may be homologous to the Clare-Bishop area in cat (Cragg and

Ainsworth, 1969; Zeki, 1969b, 1971a; Jones and Powell, 1970; Cowey, 1971). Interposed between areas V3 and V6 are at least three further areas (V4, V4A, V5), each receiving a projection from areas V2 and V3 (Zeki, 1971b; Cowey, 1973). According to Zeki (1969, 1974a) these areas lie within area 18 as defined by Brodmann. Finally V4, V4A and V5 (possibly also V6) project to the inferior temporal cortex, which may also contain a multiplicity of distinct areas (Cowey, 1971; Zeki, 1974b).

Identification of multiple secondary visual areas is dependent on the use of small cortical lesions and avoidance of damage to the underlying fibre layers. Jones and Powell's (1970) cortical connectivity study in rhesus monkey, using a modified Brodmann terminology based on connectivity patterns, involved large lesions often invading more than one visual area as defined by Zeki and others, (for example area 20 as defined by Jones and Powell corresponding at least partially with Zeki's visual areas V4 and V4A).

The existence of multiple secondary visual areas in extrastriate cortex of New World primates has been disputed by Spatz and co-workers (Spatz and Tigges, 1972; Tigges et al, 1974) who suggested there might be a species difference. However, the lesion sites in V1 used in their studies were restricted to the dorsolateral surface and tended to be larger than those used in the rhesus monkey. Connectivity studies using smaller lesions and axonal transport techniques involving both lateral and medial surfaces have, however, revealed multiple striate-extrastriate projections (Cowey, 1973; Martinez-Millan and Hollander, 1975) in New World monkeys.

In a series of electrophysiological mapping studies, Allman, Kaas and co-workers have demonstrated a multiplicity of visual field representations in extrastriate cortex of the New World owl monkey. As

earlier demonstrated in the squirrel monkey (Cowey, 1964), there was a secondary visual area (V II) forming a belt which surrounds most of V I (Allman and Kaas, 1974a) which, according to Allman and Kaas, is coextensive with a cytoarchitectonic area regarded as 'area 18' of Brodmann in this species. Anterior to V II (within 'area 19' of Brodmann) are at least five distinct visual areas which include the middle temporal area (MT: Allman and Kaas, 1971 - homologous to the posterior bank of the superior temporal sulcus), the dorsolateral visual area (DL) which forms a crescent around MT (Allman and Kaas, 1974b), the dorsomedial visual area (DM: Allman et al, 1971b,1975), the medial visual area (M: Allman and Kaas, 1974c, 1976); the dorsointermediate area (DI) interposed between DL and DM (Wagor et al, 1975) and the posterior parietal region (PP) which corresponds in location to area 7 (Wagor et al, 1975; Allman and Kaas 1976).

Cortico-cortical connectivity studies of other New World primates (marmoset and squirrel monkey) suggests that this multiple retinotopic organization may be a common feature, for lesions in V II or MT result in areas of degeneration corresponding to the locations of visual areas DM, DL and M of owl monkey (Tigges et al, 1974; Spatz and Tigges, 1972b).

Allman and others have also demonstrated the existence of visual areas MT and DL in a Prosimian species, the bush baby (Allman et al, 1973; Allman and Kaas, 1974b).

Allman and Kaas (1974a) have extensively discussed the topographical transformations of the visual field which occur in the visual system of the owl monkey, in addition to comparisons with other species. V I (as are the LGNd; inferior pulvinar, superior colliculus and MT visual area) is a simple topographical representation of the visual field which they refer to as a first order transformation of the visual field, i.e.

adjacent points in the visual field are represented as adjacent cortical loci. However the topographical transform of the visual field in V II (similarly the visual areas DL, DM and M) is different from that in V I and is referred to as a second order transformation of the visual field, in that adjacent points in the visual field are not represented as adjacent points in the cortex. The functional significance of V II as a second order transform is that it permits neuronal interaction over short axonal pathways between parts of V I and V II (similarly MT with DL and DM) representing the same portions of the visual field.

Species from a number of sub-primate orders have been used in electrophysiological mapping studies of extrastriate cortex, including: rodents - the rabbit (Thompson et al, 1950), rat (Rojas et al, 1964; Adams and Forrester, 1968), mouse (Woolsey, 1967; Drager, 1975) and the grey squirrel (Hall et al, 1971); ungulates - the domestic sheep (Clarke and Whitteridge, 1973, 1976a,b); insectivores - the hedgehog (Kaas et al, 1970) and tree shrew (Kaas et al, 1972); marsupials - the opossum (Benevento and Ebner, 1971b).

It is interesting to note that in some species (hedgehog and grey squirrel), physiologically defined visual field representations appear to correspond to the cytoarchitectonic fields 17, 18 and 19, while for other species, such as the rat (Montero et al, 1973a,b), rabbit (Woolsey et al, 1973; Montero and Murphy, 1976) and opossum (Benevento and Ebner, 1971b) there appears to be a multiple retinotopic organization similar to that found in primates.

1.7.7 Physiological considerations:

While there has been a considerable volume of comparative anatomical research, most physiological studies have been devoted to the cat and to a few of the primates.

The concentric centre-surround receptive field organization discovered in the cat (Kuffler, 1952; Hubel and Wiesel, 1961) has also been described in the retina and lateral geniculate nucleus of the rat, rabbit, ground squirrel, grey squirrel, goat, tree shrew, and a number of primate species (Brown and Rojas, 1965; Montero et al, 1968; Barlow et al, 1964; Michael, 1968a; Robson and Cooper, 1966; Hughes and Whitteridge, 1973; Sherman et al, 1975; Hubel and Wiesel, 1960, 1966).

In addition to concentrically organized receptive fields, many other types have been described, including 'local edge detectors', directionally selective units, uniformity detectors, and colour-coded units (Barlow et al, 1964; Hubel and Wiesel, 1960, 1966; Levick, 1967; Michael, 1968b,c; Montero and Brugge, 1969). Cleland and Levick (1974b) have argued that many species may possess a qualitatively similar complement of receptive field types and that species differences may be expressed quantitatively, this in some way reflecting the behavioural requirements of a given species.

The sustained and transient 'functional' classification of cells in the retina and geniculate nucleus has recently been extended to include primates (De Monasterio and Gouras, 1975; Marrocco and Brown, 1975; Marrocco, 1976; Dreher et al, 1976), the tree shrew (Sherman et al, 1975 van Dongen et al, 1976), the rat (Fukuda, 1973 - as suggested from conduction velocity data) and the goat (Hughes and Whitteridge, 1973). Dreher et al (1976) have shown, for three Macaque monkey species, that sustained (X-like) and transient (Y-like) cells appear to be segregated within the primate LGNd: sustained cells, generally exhibiting colour opponency in their receptive field organization, are located in the parvocellular layers while transient cells, with little or no colour properties, are found in the magnocellular layers. This is consistent

with previous conduction velocity studies (Doty et al, 1964; Barlett and Doty, 1974) and a recent morphological classification of retinal ganglion cells and their projections to the LGNd in rhesus monkey (Bunt et al 1975). The apparent segregation of colour-opponent and non-opponent cells in the parvocellular layers of rhesus monkey LGNd (Marrocco and Brown, 1975; Marrocco, 1976) which contrasts with Dreher et al's (1976) report. However De Monasterio et al (1976) suggest that Marrocco's 'sustained non-opponent' cells may be 'concealed colour-opponent' cells (c.f. De Monasterio et al, 1975). De Monasterio and co-workers (1976) also reported that cells classified according to their response time course to a standing contrast (sustained/transient) may not necessarily be correlated to their spatial summation (X/Y) properties - a finding also reported in the cat (Shapley and Hochstein, 1975).

The receptive fields and response properties of cells in the primary visual cortex (V I) have been studied in a variety of species including the rat (Shaw et al, 1974, 1975; Wiesenfeld and Kornel, 1975), the mouse (Drager, 1975), the rabbit (Arden et al, 1967; Chow et al, 1971), the opossum (Christensen and Hill, 1970; Rocha-Miranda, 1973; Rocha-Miranda, et al, 1976), the spider monkey (Hubel and Wiesel, 1968), the rhesus monkey (Hubel and Wiesel, 1968; Wurtz, 1969; Poggio, 1972; Baker et al, 1974; Dow, 1975; Wurtz, 1969) and in man (Marg et al, 1968; Marg and Adams, 1970). As in the cat, simple, complex and lower-order hypercomplex receptive field types are present, although a higher propertion of complex cells and non-oriented cells, compared with simple cells, are found compared with the cat. In common with the cat, physiologically defined subclasses of complex cells have been described which appear to have different laminar distributions (Hubel and Wiesel, 1968; Baker et al, 1974; Dow, 1975).

That the primate extrastriate area is a heterogeneous cortical field has been repeatedly demonstrated anatomically and electrophysiologically. Zeki (1974a) has put forward the hypothesis, based on experimental evidence to date, that different visual functions (contour, depth, movement and colour analysis) are emphasized in different anatomically defined areas. It is interesting to view this hypothesis in a more comparative context:

Contour analysis: This appears to be emphasized in V1 and every part of the visual field has a multiple representation for different orientations and contours (Hubel and Wiesel, 1975a,b,c). Colour selective cells are in a minority (7%: Hubel and Wiesel, 1968; 26%: Gouras, 1972; 30%: Dow, 1975) and cells responsive to binocular disparity have not been found (Hubel and Wiesel, 1970).

Depth analysis: In the visual area V2 about half of the cells found are complex and lower-order hypercomplex, as found in V1, the remainder are binocular disparity cells (Hubel and Wiesel, 1970; Baker et al, 1974). Some cells respond optimally when exactly corresponding retinal regions in each eye are simultaneously stimulated; others respond only when a positive or negative disparity in the receptive field positions for the two eyes is present. Cells probably involved in depth analysis utilizing cues other than disparity, appear to be found in visual areas which emphasize that particular cue, e.g. movement cues (found in the movement area in superior temporal sulcus - Zeki, 1974c).

Movement analysis: For cells in the posterior bank of the superior temporal sulcus (V6), the retinal locus is not as critical as in V1, and receptive fields are much larger (Dubner and Zeki, 1971; Zeki, 1974b). Movement appears to be particularly emphasized and cells

are responsive to motion in any or only in one direction. Other cells respond to centrifugal and centripetal movement and to jerky movement within the receptive field (Zeki, 1974b). Neither wavelength, disparity nor form appear to be critical to the cells' responses. Centrifugal and centripetal movement sensitive cells have been further studied by Zeki (1974c) and their probable involvement in depth analysis discussed. It is interesting to note that the existence of such cells has been implicated by Regan and Beverley (1973) in their investigation of evoked potentials in man.

Colour analysis: A concentration of colour sensitive cells has been reported in the fourth visual areas (V4, V4A) compared with V1, V2 and V6 (Zeki, 1973). There appears to be a large number of colour-coded cell types with different receptive field organizations and stimulus requirements. Some cells, as in V1, are selective for form, orientation and colour while others are much less selective for form. For the 'successive contrast' colour-coded cells in particular, a succession of differing wavelengths are required to elicit an optimal response. The opponent surrounds of such colour-coded cells as possess them may be arranged either symmetrically or asymmetrically. In line with Zeki's hypothesis is the psychophysical evidence for a separation of spatial and chromatic aspects of a visual stimulus (Lu and Fender, 1972). Recent clinical evidence of disturbed colour perception in patients with localized cortical lesions has implicated the existence of colour-coded areas in extrastriate cortex which may be homologous to the rhesus monkey's V4 (Meadows, 1974). Recently, Zeki (1976) has described a colour-coded area in the superior temporal sulcus lying lateral to the 'movement area' from which it is functionally distinct (receiving no striate projection and having a

unique callosal projection). There is the possibility that this colour-coded area is an extension of the colour-coded area in V4.

The apparent emphasis on different visual functions within the different anatomically defined visual areas of extrastriate cortex in primates suggests that a similar segregation of function may be present in those species where a multiple retinotopically organized extrastriate cortex has been described. In support of this view is recent evidence from Clarke and colleagues (1974, 1976) for which binocular disparity is more important for the activation of cells in V II of the sheep than in V I.

Objectives:

(i) One clear gap in the present state of knowledge of the visual thalamus is the distribution of receptive field types within the individual nuclei which comprise the LGNd complex, notably the laminated LGNd and MIN. To this end an investigation of the response properties of cells in the MIN was compared with those in the laminated LGNd, with respect to the sustained/transient classification. During this study, reports of 'sluggish' sustained/transient (W cells) became available (Cleland and Levick, 1974a,b; Stone and Fukuda, 1974). This, together with observations of cell responses in the C-layers of laminated LGNd, suggested further investigation was warranted with regard to these more recent classifications. A preliminary investigation of the cortical projections from the LGNd complex, using the recent method of retrograde transport of horseradish peroxidase (HRP), was also undertaken in an attempt to correlate any differential distribution of cell types within the LGNd complex with a differential cortical projection. These results are presented in Chapter 3 and as preliminary reports (Mason, 1975; 1976a).

(ii) While these studies were in progress, experiments in this laboratory demonstrated a differential sensitivity of simple and complex cortical cells to textured 'visual noise' (Hammond and MacKay, 1975a,b; 1976). These reports raised the question of whether a similar differentiation of cell types was present at retinal or geniculate levels. A study of the responses of cells in the LGNd complex to visual noise was undertaken, with the additional possibility that it might reveal differential responsiveness to noise, associated with the

individual nuclei of the LGNd complex. These results are presented in Chapter 4 and as a preliminary report (Mason, 1976b).

(iii) During the course of the above studies on the LGNd complex, many electrode penetrations also passed through the nuclei of the pulvinar-complex medial to the LGNd complex. Additional experiments, directed solely at the pulvinar-complex, were subsequently carried out to elaborate these incidental observations. The results are presented in Chapter 5 and discussed in context with the rest of the cat's visual thalamus and also from a comparative viewpoint in Chapter 7.

(iv) The question of whether the experimental observations are unique to the cat (as a representative of the Carnivora) was examined through an investigation of the neuronal organization present in the rat's LGNd and pulvinar-complex. The rat was chosen on economic grounds, following reports of a second representation of the visual field adjacent to the LGNd (Montero et al, 1968) - a possible homologue of the feline MIN - and following indications from conduction velocity experiments of slow and fast geniculate relay cells (Fukuda, 1973) - possibly equivalent to the sustained and transient cells described for the cat. These results are presented in Chapter 6.

EXPERIMENTAL METHODS:

Cat studies:

2.1.1. Surgical preparation:

Experiments were carried out on 49 adult cats (body wt. 1.9 to 3.5 kg; mean 2.6 kg). Preparations were used for up to three days, often being shared between colleagues (for cortical, geniculate and retinal studies) working peripherally. One of two anaesthetic preparations was used:

(i) induction with an i.p. administration (35-45 $mg.kg^{-1}$) of sodium pentobarbitone (Nembutal, Abbott), with subsequent i.p. maintainance doses (0.4 ml; 60 mg ml^{-1}) during recording as required;

(ii) induction and surgery performed under halothane (Fluothane, ICI) in oxygen. Subsequently, for recording, animals were maintained on a nitrous oxide/oxygen (N_2O/O_2) mixture (72.5%:27.5% or 75%: 25%) supplemented with small doses (0.05-0.1 ml) of sodium pentobarbitone (Nembutal, Abbott) as required (averaging $1.0mg.kg^{-1}.hr^{-1}$).

The left and right cephalic veins were cannulated for i.v. administrations and a tracheal cannula was inserted. Blood pressure was monitored using a Devices CEC transducer connected to a cannula in the left carotid artery. A continuous sodium citrate infusion (3% solution at $0.3ml.hr^{-1}$) through this cannula prevented clotting. A bilateral cervical sympathectomy was performed on cats maintained on gaseous anaesthesia. Body temperature was maintained at 38°-39°C by an electric heating blanket under the control of a rectal thermistor probe.

Cats were mounted in a modified Narishige stereotaxic frame providing minimal obstruction of the visual field. The scalp and temporales muscles were reflected and two stainless steel screws, inserted over the left or

right visual and auditory cortices, served as electrodes for the differential recording of the surface cortical EEG. The EEG was amplified through a Devices 3160 amplifier (bandpass 0.8-50 Hz) and continuously written out simultaneously with the blood pressure record on a Devices M2 2-channel pen recorder. In the majority of cats anaesthetized with N_2O/O_2 mixtures a head clamp attached to the skull by four stainless steel screws replaced the orbital and ear bars during recording. A small craniotomy (3-10 mm diameter) performed vertically over the LGNd/pulvinar nuclei (between Horsley-Clarke co-ordinates A4.0-A7.5; L5.0-L11.0) or at the appropriate position over the middle ectosylvian or suprasylvian gyri for oblique microelectrode penetrations.

On completion of the surgical procedures cats were artificially ventilated and when the end-tidal CO_2 was stable the appropriate anaesthetic scheme for maintainance during recording was adopted. For pentobarbitone anaesthetised cats the anaesthetic level was allowed to lighten as far as was consistent with satisfactory EEG and other monitoring criteria. Cats induced on halothane were transferred to a halothane-N_2O/O_2 mixture and the halothane was gradually withdrawn, the N_2O/O_2 mixture then being supplemented with small i.v. doses of pentobarbitone which abolished muscle tone and those reflexes generally present under N_2O/O_2 alone (which has been shown to be an inadequate anaesthetic in cats when used unsupplemented - Russell, 1973, Richards & Webb, 1975; and our own extensive personal experience in this laboratory - Hammond, James & Mason, unpublished; see also Hammond 1971 p.478). End-tidal CO_2 was continuously monitored with a Beckman LB1 or LB2 Medical Gas Analyser, or occasionally (in experiments with pentobarbitone anaesthesia) with a Bournes Life Systems end-tidal CO_2 monitor, and maintained at 4.0% or, in later experiments at 4.5%, using a Palmer artificial ventilator

(28 strokes min^{-1}) and continuously monitored on a Washington oscillograph (400 MD/2). Eye immobilization was provided by an initial i.v. dose (40 mg), and subsequent i.v. infusion of, gallamine triethiodide (Flaxedil, May & Baker - 20 $mg.ml^{-1}$ in 2.5% dextrose solution) at 1 $ml.hr^{-1}$. In addition, a bilateral cervical sympathectomy was performed in preparations maintained on gaseous anaesthesia, in order to reduce residual eye movements (Rodieck et al, 1967). The EEG, end-tidal CO_2, blood pressure and pulse were all assessed in relation to the reflex state of the preparation prior to paralysis, for use as criteria of adequate anaesthesia during paralysis when conventional methods are no longer possible.

2.1.2 Optics:

The pupils were dilated and nicitating membranes and eyelids retracted by the application of 1% (w/v) atropine sulphate and 10% (w/v) phenylephrine hydrochloride eye drops respectively. The corneae were protected with a pair of two-curve neutral contact lenses (Hamblin) selected from the following sets of lenses:

Base curve/peripheral curve: 8.0/8.5 mm
8.5/9.0 mm
9.0/9.5 mm

Each lens had a base diameter of 8.0 mm and a peripheral diameter of 12 mm. Selection was based on the data of Vakkur and Bishop (1963) and Vakkur et al (1963), and as described by Andrews and Hammond (1970). Dissociation between the EEG and the behavioural state following administration of atropine has been reported (Bradley, 1958); eye drops were therefore withheld in some preparations to establish that, in the concentrations used, no dissociation occurred.

Focal correction was assessed retinoscopically and by the subsequent performance of single cells in the LGNd complex (after Cleland et al. 1971b) for the various stimulus distances used (i.e. 57.3 inches, 85 or 50 cm from the nodal points of the eyes). Trial lens spheres were placed in front of the eyes, as necessary. Projections of the optic discs and areae centrales were monitored by back-projection with an ophthalmoscope (Keeler) and corner cube prism or by the method of Fernald and Chase (1971). A range of circular artificial pupils was available (2-6 mm in diameter) and 5 mm pupils were routinely used. Care was taken to ensure they were centred over the area centralis.

The retinae were routinely checked ophthalmoscopically to ensure that the optic media were clear (any corneal clouding was cleared by topical application of hypertonic (3%) saline) and the retinae scanned for abnormalities. In two cats feline central retinal degeneration was found (Bellhorn & Fischer, 1970; Bellhorn et al, 1974), consisting of focal lesions approximately 1 mm in diameter which included all or most of the area centralis. In these cats electrode penetrations were made in that portion of the LGNd complex where the peripheral visual field (15°-35°) was represented, a region of the retina not apparently occupied by the lesion, in addition to the medial edge of the LGNd complex where the central visual field is represented. Cells recorded in 'peripheral' laminated LGNd were similar to those recorded in normal cats. However no cells with receptive fields occupying the central 4° of the visual field could be found. Subsequent histology showed some cell loss along the medial edge of the laminated LGNd where central vision is represented.

2.1.3. Recording:

Extracellular recordings from single cells in the LGNd complex and

nuclei of the pulvinar complex were made with glass micropipettes filled with 2-4% Pontamine Sky Blue (Gurr 5BX) dissolved in 0.5M NaCl. With tip diameters between 1.5 - 3.0 μ, the impedance was typically 3 - 10 MΩ. For some penetrations, glass micropipettes containing 4M NaCl, or tungsten-in-glass electrodes (Levick, 1972) were used to provide some check on the recording characteristics of the dye-filled micropipettes. Dye-filled micropipettes were advantageous when reconstructing electrode tracks, but tended to isolate spikes with a poorer signal-to-noise ratio than the other types of electrode; tip diameters of 2.5-3.0 μ were found to provide the best cell isolation.

Electrode penetrations were made through small craniotomies (see sections 2.1.1., 3.1.1), the dura having been previously removed. Electrodes were advanced mechanically to a depth of 10-12 mm from the cortical surface and sealed with 2% (w/v) immuno-agar (Oxoid) pre-cooled to 39°C to reduce pulsation and covered with a layer of low melting point wax to prevent dehydration. Subsequent electrode advance was under the control of a hydraulic microdrive.

Signals were fed through a FET input-stage unity gain follower (Ancom 15B-2), amplified by an Isleworth Electronics A101 preamplifier (bandpass 0.2-5 kHz) and displayed conventionally on a Tektronix RM565 oscilloscope. A window-discriminator allowed separation of positive or negative polarity spikes and spikes of differing amplitude from the background noise. Z-modulation was used to intensify the discriminated portion of the spikes or the complete spike for photographic purposes. Discriminated spikes were monitored aurally and, as standard 1 μsec pulses, were fed to electronic counters (Advance TC11A or Venner TSA6634) appropriately gated for delay and duration. They were also led to a data retrieval computer (Biomac 1000) for compilation of peri-stimulus

time histograms (PSTH's). The raw data were stored on magnetic tape (Thermionics T3000 four channel FM tape recorder) for off-line analysis.

2.1.4. Visual stimulation:

Four methods of presenting visual stimuli were available:

(i) hand-held wands: these consisted of black or white discs and slits of various sizes, made from card, and a series of parallel grating and radial grating patterns;

(ii) a rear-projection system (after Barlow et al, 1967) which enabled the generation of both light or dark stimuli (discs, slits and edges) on a tangent screen;

(iii) front-projection onto a matt white tangent screen, using two modified Rank-Aldis Tutor 2 projectors, fitted with Atlas A1/223, 24 volt, 250 watt tungsten-halogen projection lamps. A variety of spot, annular and slit stimuli, of various dimensions, and parallel grating patterns, with a range of spatial frequencies were available in slide form. Flashed stimulus presentations were provided by pendulum shutters driven by Ling Altec V47 vibration generators and were monitored using a photodiode (R.S. Components). The projectors were positioned on either side of the cat and were pivoted about horizontal and vertical axes, which allowed manual scanning of the visual field. Two pivoted mirrors in front of each projector lens, enabling fine control of stimulus position, were driven by vibration generators (Ling Altec V47) which could be under remote manual control. Application of triangular waveforms to the vibration generators provided linear stimulus motion, excursion 12°, at velocities up to

120° sec^{-1}. Kodak Wratten neutral density filters allowed the stimulus intensity to be reduced in calibrated steps of approximately 0.1 log units over a range of 4 log units. A range of background adapting levels from -1.57 log $cd.m^{-2}$ to +1.56 log $cd.m^{-2}$ was available. During this study, background adaptation was +1.24 log $cd.m^{-2}$ which, in conjunction with 3 or 5 mm artificial pupils, is mid- to high-mesopic for the cat (Hammond and James, 1971; Ahmed and Hammond, In preparation).

(iv) In later experiments a CRT display was used (MacKay and Yates, 1975; Hammond and MacKay, in preparation). This consisted of a Hewlett-Packard 1300A display operating with a rectangular raster of 256 x 256 black/white elements, repeating at 50 or 200 frames sec^{-1} and modified to allow rotation of the picture through 180° by means of analogue circuitry using a sine-cosine potentiometer. Z-modulation derived from digital hardware provided a movable and rotatable 'figure' of variable shape (including light or dark bars), random visual 'noise' (either static or dynamic) or dot/line arrays; and a light/dark contrast, or noise (static or random) background independent of the figure. The 'figure' or background could be flashed or moved back and forth synchronously, and so enabling generation of PSTH's. Receptive field mapping was carried out with the aid of a plotting table onto which visual stimuli (and the locations of optic discs and areae centrales) were transferred by a parallax-free optical system.

2.1.5. Electrical stimulation:

Stimulating electrodes were a pair of stainless steel wires insulated

with polyurethane varnish, the tips of which were bare for 1 mm and 3 mm apart. The electrode pair was placed stereotaxically in the optic chiasm (Horsley - Clarke co-ordinates A 13-14; LL 2.0 RL 2.0; and 22-24 mm below the cortical surface). Final electrode depth was determined while recording through the stimulating electrode during visual stimulation or recording the field potential in the LGNd complex to 50 μsec pulses as the electrode pair was lowered.

Electrical stimuli were 50 or 100 μsec duration pulses from Tektronix 161 pulse generator, delivered through a Devices Mk IV isolated stimulator.

2.1.6. Histology:

Marking of the electrode position was achieved by electrophoretic ejection of Pontamine Sky Blue dye (5-10 μA for 5-10 min; electrode tip negative). At the termination of the experiment the animal was deeply anaesthetized with sodium pentobarbitone and perfused intra-arterially with 10% formol saline, allowed to fix for up to 24 hours and slices containing the electrode tracks removed. These slices were then sectioned at 50μ on a freeze microtome (MSE) and stained with cresyl-violet. Sections were examined, photographed (using a Nikon multiphot system) and electrode tracks were reconstructed with the aid of identified dye marks onto outline drawings of the LGNd complex (and pulvinar nuclei when appropriate).

2.1.7. Horseradish peroxidase (HRP) study:

Five cats were used to investigate the projections from the LGNd complex to areas 17 and 18 of visual cortex using the method of retrograde axonal transport of HRP after the method of Graybiel and Devor (1974) and Lynch et al (1974). Glass micropipettes with tips chipped to 20-25 μ were

back-filled with a 5% or 10% solution of HRP (Sigma Type II or VI) in either 4M NaCl or 0.05M Tris-HCl buffer (pH 8.6). HRP ejection was achieved by passing a positive current of 2-5 μA for a period of 15-45 min. delivered as 0.5 Hz square wave pulses. HRP-micropipettes were found to be suitable for multi-unit recording, enabling the characterization of the injection site. Prior to HRP injection, areas V I and V II were briefly characterized electrophysiologically; a reversal in the trend of receptive field azimuth as penetrations were made successively in a lateral direction and the presence of larger receptive fields (i.e. minimal response fields - Barlow et al, 1967) indicated that the electrode was situated in V II. Injection sites in V I were at Horsley-Clarke co-ordinates P1-5, L1-2 and those in V II were at co-ordinates A3-P2, L3-4. Post-injection survival periods ranged between 20-30 hours.

Animals were perfused with 500ml of 4% paraformaldehyde or a 0.5% paraformaldehyde-2.5% glutaraldehyde solution in 0.1M phosphate buffer (at 4°C); the latter solution was found to give the best results. Sections of brain containing the LGNd complex and the injection sites were then removed and stored in the perfusate at 4°C overnight and then transferred to 0.1M phosphate buffer (pH 7.6) containing 5% sucrose at 4°C for 24 hours. Frozen sections (50 μ) were reacted according to the method of Lynch et al (1974 - after that of Straus, 1964) or Graybiel and Devor (1974 - after that of Graham and Karnovsky, 1966). The method of Lynch and co-workers (using HRP, Sigma Type II) was found to give poorer results than a modification of Graybiel and Devor's (1974) method. The modified histochemical procedure consisted of incubating the sections with 0.05 or 0.1% o-dianisidine HCl (Sigma D3252) in 0.05M Tris-HCl buffer (pH 7.6) for 20 min., then transferring to a similar solution containing 0.3% H_2O_2 for a further 30 min. at 37°C. Sections were then rinsed three times in

distilled water and mounted onto glass slides from a gelatin-alcohol mixture, air dried, dehydrated through an ascending series of alcohol solutions, cleared and cover-slipped (in some cases sections were lightly counterstained with cresyl-violet prior to microscopy). Sections were then examined in the light microscope under dark field illumination for HRP-positive cells and their location mapped (from the microscope stage micrometer readings). HRP-positive sections were lightly stained with cresyl-violet, after cover slip removal, enabling nuclear boundaries containing the HRP-positive cells to be mapped. Sections were also examined under higher magnifications with bright illumination for the brown granular reaction product in the cell cytoplasm; in many cases the granules were difficult to detect in stained sections.

Rat (Rattus norvegicus) studies:

Two strains of rat were used in the study - the Wistar albino variety (6) and the Lister black hooded rat (15). The hooded rats were supplied by Drs. J.L. Smart and A. Lynch (Department of Child Health, University of Manchester Medical School). These consisted of undernourished (foetal and early postnatal undernutrition) and control litters (reared as described by Smart and Dobbing, 1971), which had previously been used to investigate the motor performance of adult rats undernourished in early life. In passing, such studies have shown that there is a motor co-ordination deficit which could be correlated with histological changes in the cerebellum (Lynch et al, 1975).

2.2.1. Preparation:

Rats were anaesthetized by one of three methods having been fasted for 12 hours but allowed water ad libitum:

(i) an i.p. injection of sodium pentobarbitone (Nembutal, Abbott; 30-35 $mg^{1}.kg^{-1}$ - 4 rats) with additional doses as necessary.

(ii) An i.p. injection of urethane (130 $mg.100g^{-1}$ - 4 rats) with additional doses as necessary.

(iii) 'Neuroleptanaesthesia' (after the method of Evans, 1976 - 13 rats): sodium pentobarbitone (Nembutal, Abbott; 30 $mg^{1}.kg^{-1}$) was administered i.p. and atropine sulphate (0.06 mg) was given sub-cutaneously. After about 15 minutes a mixture of droperidol (4 $mg^{1}.kg^{-1}$ - Janssen Pharmaceuticals) and phenoperidine (1 $mg.kg^{-1}$ - Janssen Pharmaceuticals) was given i.p. Sufficient analgesia and hypnosis ensued within 15-20 minutes for surgery to commence. Maintenance of anaesthesia during recording required i.v. injections of sodium pentobarbitone (3 $mg.kg^{-1}$ every 2 hours, indicated by a sudden rise in blood pressure) and i.v. phenoperidine (1$mg.kg^{-1}$) every hour, indicated by a withdrawal reflex to pinching the paw.

A tracheal cannula was inserted, the carotid or femoral artery cannulated in order to monitor the blood pressure, and the femoral vein was cannulated for i.v. administrations. Physiological monitoring (i.e. end-tidal CO_2; blood pressure; rectal temperature) was similar to that described earlier for the cat.

The rat was mounted in a specially designed head-holder (modified after Hosko, 1972) which permitted exploration of most of the rat's visual field (only the central 60° was studied). The head-holder was attached to the stereotaxic frame and, prior to mounting the rat, was

calibrated with a rat skull to correspond to the orientation appropriate for the stereotaxic atlas of König and Klippel (1963). A craniotomy (5-7 mm) was performed on the dorsal portion of the parietal bone over the lateral geniculate and lateral posterior nuclei (between 3-7 mm from the intersection of the lambdoidal and saggital sutures and 2.5-3.5 mm lateral to the saggital suture. A dam of plasticine was built up around the craniotomy which, after the insertion of an electrode, was filled with 2% (w/v) immuno-agar. In later experiments a perspex recording cylinder was cemented over the craniotomy with dental acrylic. A metal ring attached to the recording chamber, itself clamped to the stereotaxic frame, served to support the animal's head.

A wire ring attached to the head-holder was pressed around the eyeball to immobilize the eye. The eyes were protected by allowing a small drop of silicone fluid to spread over the surface of the cornea. This was repeated as required. Projections of the optic discs (approximately 70° lateral to the midline and 25° above the horizontal) using back-projection with an ophthalmoscope and corner-cube prism served to monitor eye movements and as landmarks for comparing the data from different animals. No midriatics were used and the pupil was constricted throughout. The background illumination was between -0.24 log $cd.m^{-2}$ and +0.53 log $cd.m^{-2}$.

The refractive state of the rat's eye determined by ophthalmoscopy has been reported by some authors to be hypermetropic, with refractive errors of between 7 and 17D (Block, 1969; Massof and Chang, 1972; Shaw et al, 1975). Other investigators have reported that the rat is a myopic animal (Lashley, 1932, 1937; Brown and Rojas, 1965; Montero et al, 1968; Wiesenfeld and Kornel, 1975; Wiesenfeld and Branchek, 1976). Retinoscopy performed on species with small eyes (e.g. the rat) results in an error of apparent severe hypermetropia, an error probably due to the distance between the light reflecting layer and the receptor layer (Glickstein and

Millodot, 1970). Visual stimuli were presented by rear-projection at 30 or 40 cm, or on a CRT display at 40 or 50 cm as described in section 2.1.4. These distances have been used by other workers (Brown and Rojas, 1965; Montero et al, 1968; and Wiesenfeld and Korner, 1975); moreover receptive field sizes of retinal ganglion cells were their smallest when measured at 40 cm. No attempt was made to correct for focus on the screen since depth of focus in such a small eye was assumed to be large (Hughes, 1974); further correction with ophthalmoscopic methods would prove too difficult. However, focal correction was assessed from the performance of isolated LGNd cells to parallel grating patterns and when the pupil was small (i.e. having withheld midriatics). Cellular discharge 'acuity' tended to be maximal for the stimulus distances used, further indicating a large depth of field with a small pupil.

Extracellular recording was identical to that for the cat (2.1.3.), using either glass pipettes containing Pontamine Sky Blue or tungsten-in-glass electrodes. Similarly, histological procedures were identical to those described earlier for the cat.

Chapter 3

LGNd-COMPLEX I: NEURONAL ORGANIZATION (ELECTROPHYSIOLOGICAL STUDY)

3.1. Procedure:

The results are based on the data from a total of 736 cells recorded from the LGNd complex (476 laminated LGNd; 231 MIN) and the PGN (29). Cells and fibres were distinguished on the criteria of Bishop et al (1962a,b); only cells were included in this sample.

Electrode penetrations were made stereotaxically between Horsley-Clarke co-ordinates A4.5 - A8.0; RL6.0 - 10.0 according to a stereotaxic atlas (Snider & Niemer, 1961) and visual field projection maps (Sanderson, 1971). A pilot penetration (A6.0, RL9.0) provided a reference for subsequent penetrations, determination of the vertical meridian (after Sanderson & Sherman, 1972) and control for electrode sampling bias.

Both eyes were unmasked during the initial search period for units. A large (10°) flashed stimulus (projected onto the tangent screen or generated on the CRT display) and hand-held wands were used to search for units while listening to the audio-monitor for the background "geniculate-swish". Having determined the approximate position in the visual field for driving units (the LGNd complex being retinotopically organized), individual units were isolated by manipulation of the hydraulic micro-drive using smaller (1°-2°) flashed stimuli. On isolation of a unit the driving eye was determined and the non-driving eye occluded. On- or off-centre characteristics were established with wands and flashed light or dark

stimuli (spots and bars). Receptive field centres were plotted as a contour of iso-sensitivity to a small spot onto sheets of matt white paper attached to the tangent screen, or CRT plotting table(see 3.2.6).

Once the receptive field positions of the first few units had been determined in layers A and A_1 it was possible to:

(i) determine the zero vertical meridian (accurate to ±1°) by the receptive field separation method described by Sanderson and Sherman (1972). The distance from the centre of the blind spot (Y) is given by the expression

$$Y = \frac{A - \bar{F}}{2}$$

where A = the blind spot separation

$\bar{F}$ = the average receptive field separation of pairs of receptive fields, one in layer A and the other in layer A_1;

The zero vertical meridian determined by this method passed within 0-1.5° of the ophthalmoscopic projection of the area centralis.

(ii) estimate from the visual field projection maps of Sanderson (1971) the relative position of the electrode in the LGNd and plan subsequent electrode penetrations accordingly.

One of three approaches was used for subsequent electrode penetrations: (a) a series of vertical penetrations placed progressively more medially; (b) an oblique penetration (in a coronal plane) at 50°-60° with respect to the vertical stereotaxic plane; or (c) an oblique penetration (in a coronal plane) 5-10° from the point where the pilot penetration entered the cortical surface. The oblique penetrations passed sequentially through the laminated

LGNd and MIN allowing investigation of any vertical organization that might be present in the MIN. In all approaches, reversal in trend of azimuth indicated that the electrode had entered the MIN, the location of which was subsequently confirmed histologically. A greater range and rate of change of receptive field position was generally observed for MIN units compared with those recorded from the laminated LGNd.

3.2. Sustained/transient classification:

Cells were classified as either sustained or transient as described by Cleland et al (1971b) and Hoffmann et al (1972). Later, sustained and transient cells were further sub-classified as either 'brisk' (X and Y cells) or 'sluggish' (concentric W-cells) as described by Cleland and Levick (1974a) and Stone and Fukuda (1974).

3.2.1. Receptive field properties:

The shape and amplitude of extracellularly recorded spikes and the spontaneous firing rate provide clues to classification. Transient cells tended to exhibit a low resting discharge (0.5-30 spikes sec^{-1}; mean 9) and yielded large amplitude spikes recordable over a considerable electrode traverse. Sustained cells generally showed higher resting discharge (5-50 spikes sec^{-1}; mean 26) and had spikes of smaller recorded amplitude.

3.2.2. Response to standing contrast:

An optimally sized spot of light (approximating the plotted receptive field centre size) was flashed on the receptive field centre, for 0.5 sec every 1.5 sec and PSTH's for sixteen presentations

accumulated. Individual responses to the same spot of light, presented for 30sec., were also examined. Such stimuli elicited an initial burst of spikes (the phasic component of the response) in both sustained and transient cells, which was followed by an elevation of the maintained firing rate (the tonic component of the response). The tonic component remained elevated for the duration of the stimulus in sustained cells. Differences between sustained and transient cells became apparent following visual inspection of their PSTH's accumulated to flashed light presentations (Figs. 4,5,6). The tonic component of the response of on-centre sustained cells decayed only slightly over the stimulus duration while at stimulus offset there was a marked suppression of the resting discharge. The maintained discharge in off-centre sustained cells during light penetrations ceased for the duration of the stimulus with an elevated maintained discharge at offset which soon decayed to the resting level. On-centre transient cells displayed a large initial transient (phasic component) followed by a less prominent tonic component which decayed much more rapidly than that found in on-centre sustained cells, with only a slight suppression at stimulus offset. Off-centre transient cells were characterized by a brief suppression of firing at stimulus onset and a strong transient response at stimulus offset with a rapid decay of any tonic component when present.

Distinction between sustained and transient cells was often difficult in off-centre cells when using flashed spots of light. Thus for all off-centre cells a black spot was presented (either as a wand or generated on the CRT display). These yielded responses and PSTH's identical to those of on-centre cells using light spots, e.g. the off-centre sustained cell (b) in Fig. 4 has a PSTH accumulated for

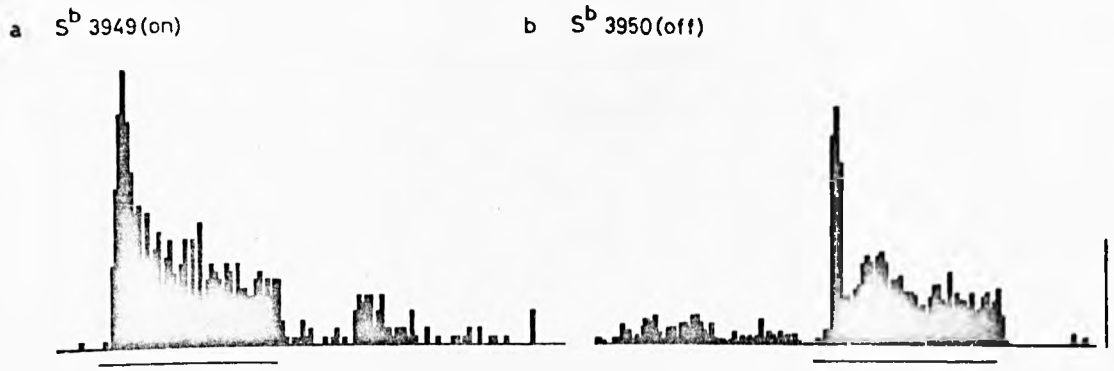
Fig. 4.

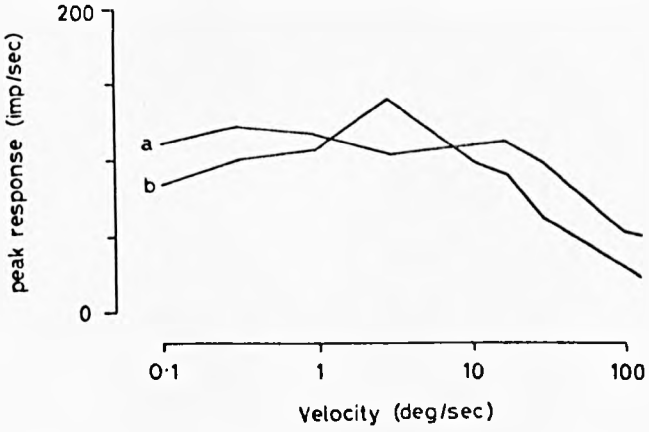
(upper) PSTH's for an on- and an off-centre 'brisk' sustained cell, recorded from layer A of laminated LGNd, accumulated over 16 consecutive presentations of an optimally sized light or dark square (appropriate to the receptive field centre) generated on the CRT display, positioned over the receptive field centre. Bin width 10.24 msec; vertical bar calibration 50 impulses/bin; horizontal bar represents duration of stimulus presentation (500 msec.)

(middle) Velocity tuning curves for the above cells. The stimuli were light or dark squares of contrast appropriate to the receptive field surround of the given cell and approximately twice the twice the receptive field centre diameter.

(lower) Flicker response curves for the same cells.

brisk sustained (laminated LGNd)





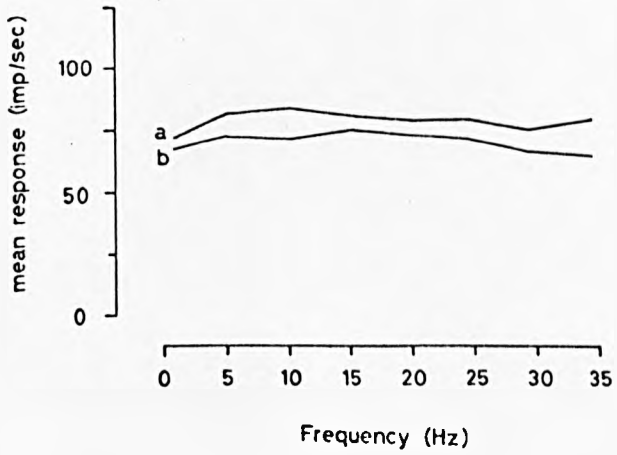


Fig. 5.

PSTHs to standing contrast to a light spot and tuning curves for velocity and flicker for on- and off-centre 'brisk' transient cells recorded from the layers A and A_1 of laminated LGNd. Details as in Fig. 4.

brisk transient (laminated LGNd)

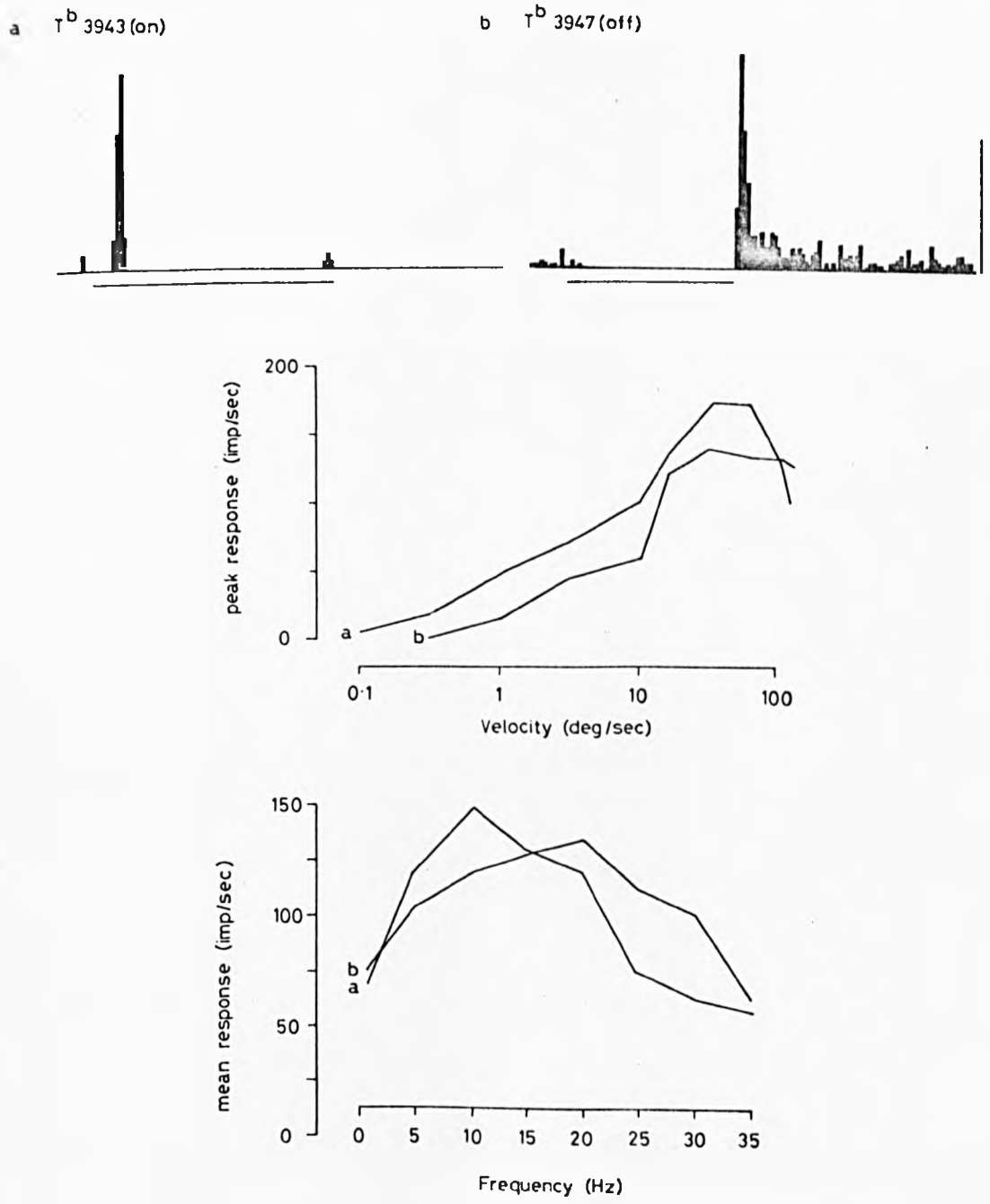


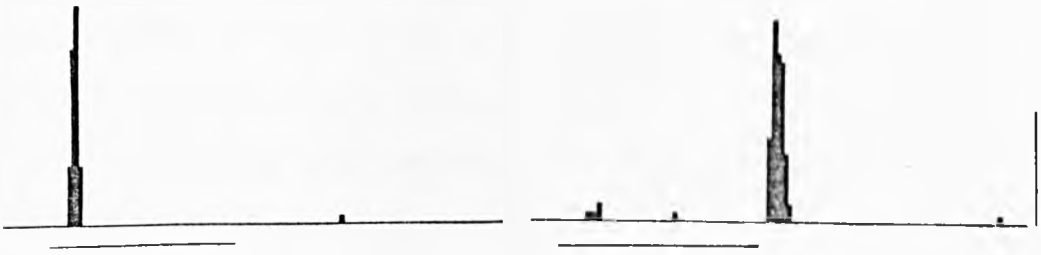
Fig. 6.

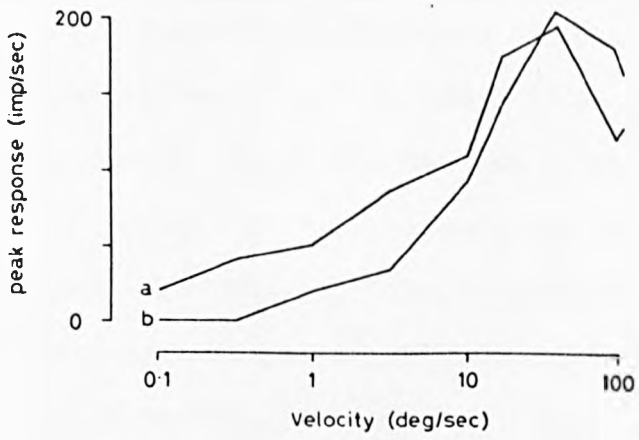
PSTHs to standing contrast to a light spot and tuning curves for velocity and flicker for on- and off-centre 'brisk' transient cells recorded from the MIN. Details as in Fig. 4.

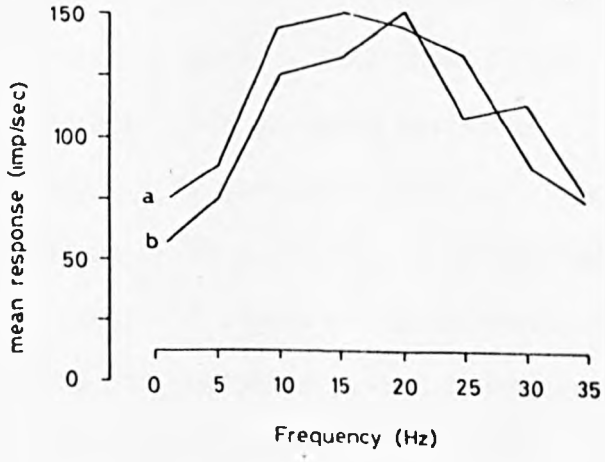
brisk transient (MIN)

a T^b 3627 (on)

b T^b 3630 (off)







presentations of a dark stimulus.

A further problem often encountered when using standing contrast in differentiating sustained and transient cells, particularly in the N_2O/O_2 preparations, was the duration of the tonic component in the response from transient cells (see off-centre transient cell (b) in Fig. 5). For a stimulus duration of 0.5 sec this did not always decay to the resting level. The use of light or dark, optimally sized spots, of contrast appropriate to the receptive field centre, and presented for 30-60 sec., avoided this difficulty.

3.2.3. Response to grating patterns:

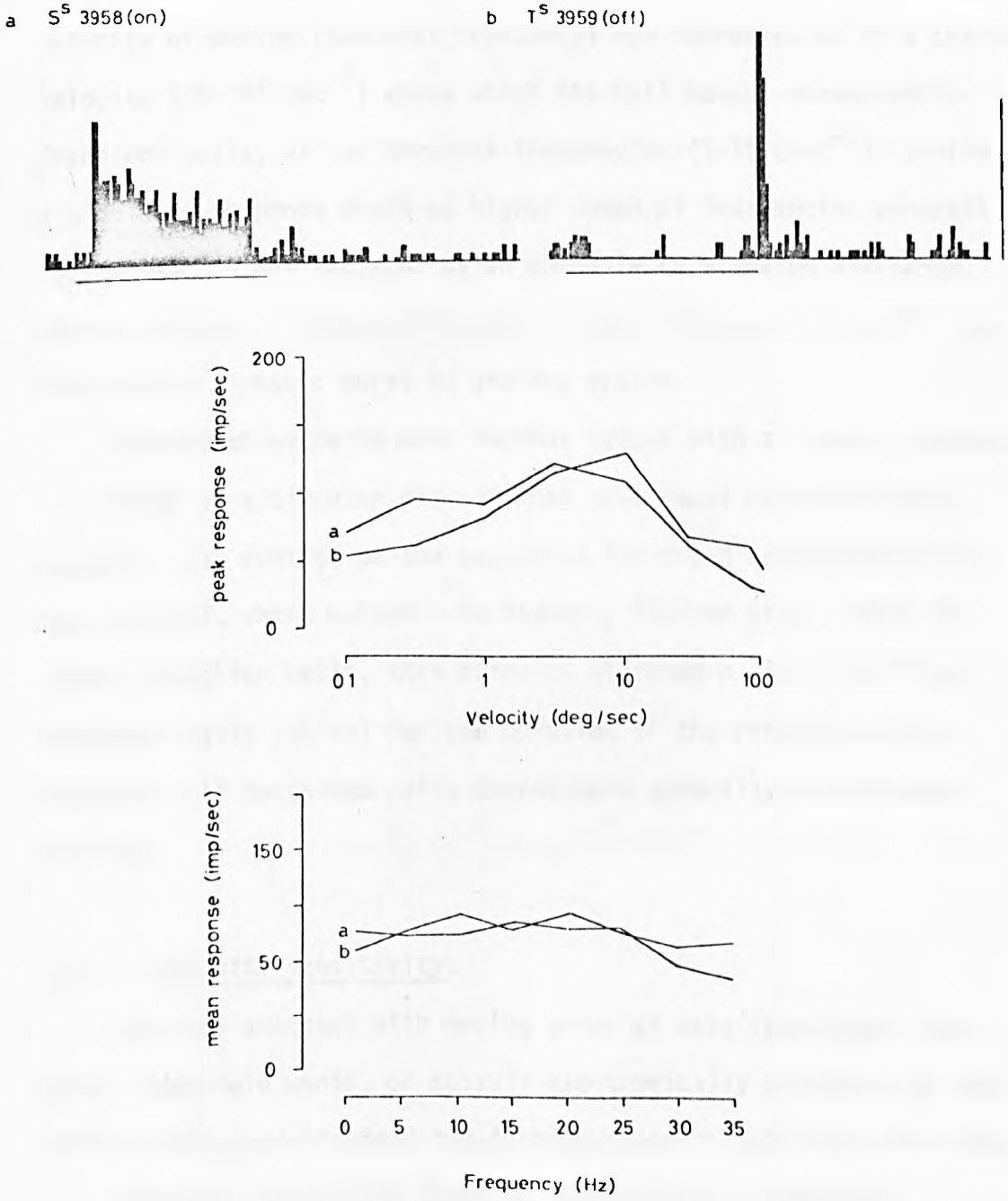
Sustained and transient cells were further characterized by their response to motion of square wave grating patterns across their receptive fields when varying either the spatial frequency at constant temporal frequency, or vice versa.

At a constant temporal frequency of 2-3 cycles/sec. both sustained and transient cells responded to low spatial frequency (coarse) gratings (less than 1 cycle/degree) with a modulated discharge about their maintained firing rate, i.e. responding at each cycle of the grating. With progressively higher spatial frequency gratings sustained cells exhibited progressively less modulated responses until reaching a 'cut-off' frequency of 3-5 cycles/degree, which appeared to be related to receptive field eccentricity, at which the discharge was unmodulated. However, for transient cells, at higher spatial frequencies (1-3 cycles/degree) the modulated response was replaced by an unmodulated elevation of discharge during grating motion. At still higher spatial frequencies (3-6 cycles/degree) transient cells responded phasically only at the on-set of grating

Fig. 7.

PSTHs to standing contrast to a light spot and velocity and flicker tuning curves for an on-centre 'sluggish' sustained and an off-centre 'sluggish' transient cell recorded from layer C (parvocellular) of laminated LGNd. Details as in Fig. 4.

sluggish sustained/transient (laminated LGNd)



motion.

For a constant spatial frequency up to 3 cycles/degree it was possible to differentiate sustained and transient cells by varying the temporal frequency of grating motion. The modulated response of sustained cells to grating motion was progressively reduced when the velocity of motion (temporal frequency) was increased up to a cut-off velocity (20-30°.sec^{-1}) above which the cell became unresponsive. Transient cells, at low temporal frequencies (1-15°.sec^{-1}), yielded a modulated response which at higher temporal frequencies generally (10-30°.sec^{-1}) was replaced by an unmodulated elevated discharge, which in turn (at temporal frequencies usually above 30°.sec^{-1}) was followed by a phasic burst to grating motion.

Seventy-three cells were further tested with a 'radial grating', consisting of a circular disc divided into equal black and white segments, was centred on the receptive field and rotated manually with a brief, sharp motion. As found by Cleland et al (1973) for retinal ganglion cells, this stimulus elicited a discharge in all transient cells (40/40) for the duration of the rotation, while virtually all sustained cells tested were generally unresponsive (31/33).

3.2.4. Velocity sensitivity:

This was assessed with moving discs or bars (projected light spots, hand-held wands, or stimuli electronically generated on the CRT display), and provided two further clues to cell classification.

When the size of the stimulus was varied, the response increased initially and then decreased with increasing stimulus dimensions. The optimal stimulus diameter correlated well with

receptive field centre size - less than 1° for sustained cells and 1-4° for transient cells.

Sustained and transient cells were differentiated with a stimulus of optimal or twice optimal dimensions, provided the stimulus contrast was appropriate to the receptive field surround (e.g. a white disc for an off-centre cell). Both cell types generally responded at low (1-5°.sec^{-1}) and moderate (20-50°.sec^{-1}) velocities, whereas at high velocities (greater than 100°.sec^{-1}) only transient cells were responsive (Figs. 4,5 and 6). Occasionally, transient cell responses were weak or absent at low velocities Figs. 5 and 6. Sustained cells with receptive fields near the area centralis (receptive field centre size 0.25-0.5° diameter) were often only responsive to slowly moving stimuli. While the range of velocity preferences overlapped for sustained and transient cells there was a tendency for velocity preference to be related to receptive field centre size. If the stimulus contrast was appropriate to the receptive field centre it was found that many sustained cells (84/131) could be driven at high velocities (greater than 100° sec^{-1}), comparable with those of transient cells. With stimuli of such contrast it was impossible to reliably distinguish between sustained and transient cells.

3.2.5. Periphery effect:

Movement of a large contrasting pattern, either a grating or a wand consisting of an irregular arrangement of strips of black tape on white card (11° x 11°), beyond the cell's receptive field centre (more than 20°) was used to elicit the periphery effect. This comprised a gradual elevation or suppression of the cell's maintained

firing rate in the majority of transient cells, and was weak or absent in sustained cells. The magnitude of the response varied in different transient cells; where the response was weak it could be intensified by presenting a stationary light spot over the receptive field.

The periphery effect appeared to be more prominent in N_2O/O_2 preparations than in pentobarbitone preparations. This was demonstrated in one cat under N_2O/O_2 anaesthesia when the discharge rate for three transient cells was compared before and after a small intravenous dose (4 mg kg^{-1}) of pentobarbitone (i.e. a higher dosage than used for N_2O/O_2 supplementation).

3.2.6. Receptive field centre size:

Receptive field centres were plotted as a contour of iso-sensitivity to a small spot of light (0.25°-1.0° in diameter, the optimal size depending on the class of cell and size of receptive field, as determined roughly with moving stimuli - see section 3.2.4.) presented for 500 msec.sec^{-1}. The mapping technique consisted of the estimation of threshold for the most sensitive point within the receptive field centre, based on auditory and visual cues, and comparisons of gated spike counts over similar periods during and following each stimulus presentation. Stimulus intensity was then increased by 1 log unit and, using threshold criteria, a contour of iso-sensitivity around the receptive field centre was determined. The procedure was repeated to ensure reproducibility.

The majority of both sustained and transient cells tended to have slightly elliptical receptive field centres although tangent screen corrections were not determined, and the major axis was used to compare RFC sizes. The receptive field centres for sustained cells

were smaller (0.25-2.0°) than those of transient cells (0.5-4.0°), receptive field centres increasing in size with retinal eccentricity from the area centralis see Fig. 8. Within the sustained and transient classes RFCs of on-centre cells tended to be smaller than off-centre cells.

3.2.7.

Receptive field properties ('brisk'/'sluggish' distinctions)

It had become apparent during the study that the responses of cells in layers C and C_1 were different in some qualitative respects from those recorded in the A-laminae. Cells were, in general, less responsive to visual stimuli and tended to possess receptive field centres greater than 2° in diameter.

A reinvestigation of the functional properties of LGNd cells, in particular those in the C-laminae, was undertaken. This followed descriptions of 'sluggish' sustained and transient cells (Cleland & Levick, 1974a,b) which are equatable with the concentric w-cells of Stoke and Fukuda (1974). The properties of these 'sluggish' cells bore some resemblance to the aforementioned responses of cells in the C-laminae. Distinguishing characteristics with regard to receptive field properties were found to be, in general, rather subtle.

3.2.8. Response to standing contrast:

'Brisk'/'sluggish' differentiation on the basis of responses to standing contrast alone was rarely found to be conclusive, particularly for off-centre sustained and on-centre / off centre transient cells (compare Figs. 4,5,6 and 7). On-centre 'brisk' and 'sluggish' sustained cells were often distinguishable by visual

inspection of their respective PSTH's. At light onset the initial phasic burst of spikes in the response was less pronounced for 'sluggish' cells and in some cases was absent, despite careful focusing of the eye and centring of the stimulus spot. Post stimulus suppression at stimulus offset, often seen in 'brisk' cells, was a rarely observed characteristic of 'sluggish' cells (Fig. 7). Further, optimal responses in 'sluggish' sustained cells were obtained with 1-2° diameter spots of light while 0.25-1° spots were optimal for 'brisk' sustained cells.

Off-centre sustained cells were more difficult to differentiate into 'brisk' or 'sluggish' classes. A black disc of 1-2° in diameter produced optimal responses in 'sluggish' cells compared with dimensions of 0.5°-1.5° for 'brisk' cells. Post stimulus suppression at stimulus offset was generally absent in PSTH of off-centre 'sluggish' cells.

The only clue in distinguishing between 'brisk' and 'sluggish' transient cells was provided by inspection of the spike discharge on the oscilloscope monitor using a slower time base. There was a tendency for the spike burst in 'brisk' transient cells to be more tightly packed, which appeared to produce a crisper sound over the audio-monitor. Little, if any, differences between 'brisk' and 'sluggish' transients was apparent from inspection of their PSTH's (compare Fig. 7 with Figs. 5 and 6). Again, as for 'sluggish' sustained cells, stimuli of 1°- 2° in diameter produced optimal responses from 'sluggish' transient cells but these dimensions were comparable with the optimal stimulus sizes for 'brisk' transient cells.

3.2.9. Response to grating patterns:

Responses of sluggish cells to moving (parallel) grating stimuli, both for 'sluggish' sustained and for transient cells, consisted of a weak modulation of the discharge which became more feeble as either the spatial or temporal frequency of the stimulus was progressively increased. In five 'sluggish' sustained cells (5/43 - 3 on-centre, 2 off-centre types) grating motion resulted in a suppression of the maintained discharge.

In later experiments a radial grating was used and proved effective in most cases in distinguishing between 'brisk' and 'sluggish' transient cells, as only the former were responsive to a brief, sharp rotation of the grating when centred over the receptive field.

3.2.10. Velocity sensitivity:

When tested with moving spot or bar stimuli most 'sluggish' cells behaved like their 'brisk' counterparts in responding to both light and dark stimuli. Some cells appeared to have a preference for motion of stimuli with a contrast appropriate to the receptive field centre (i.e. dark stimuli for off-centre and light stimuli for on-centre cells). For a few cells (4/43) movement of a stimulus of opposite contrast resulted in suppression of the cell's maintained discharge.

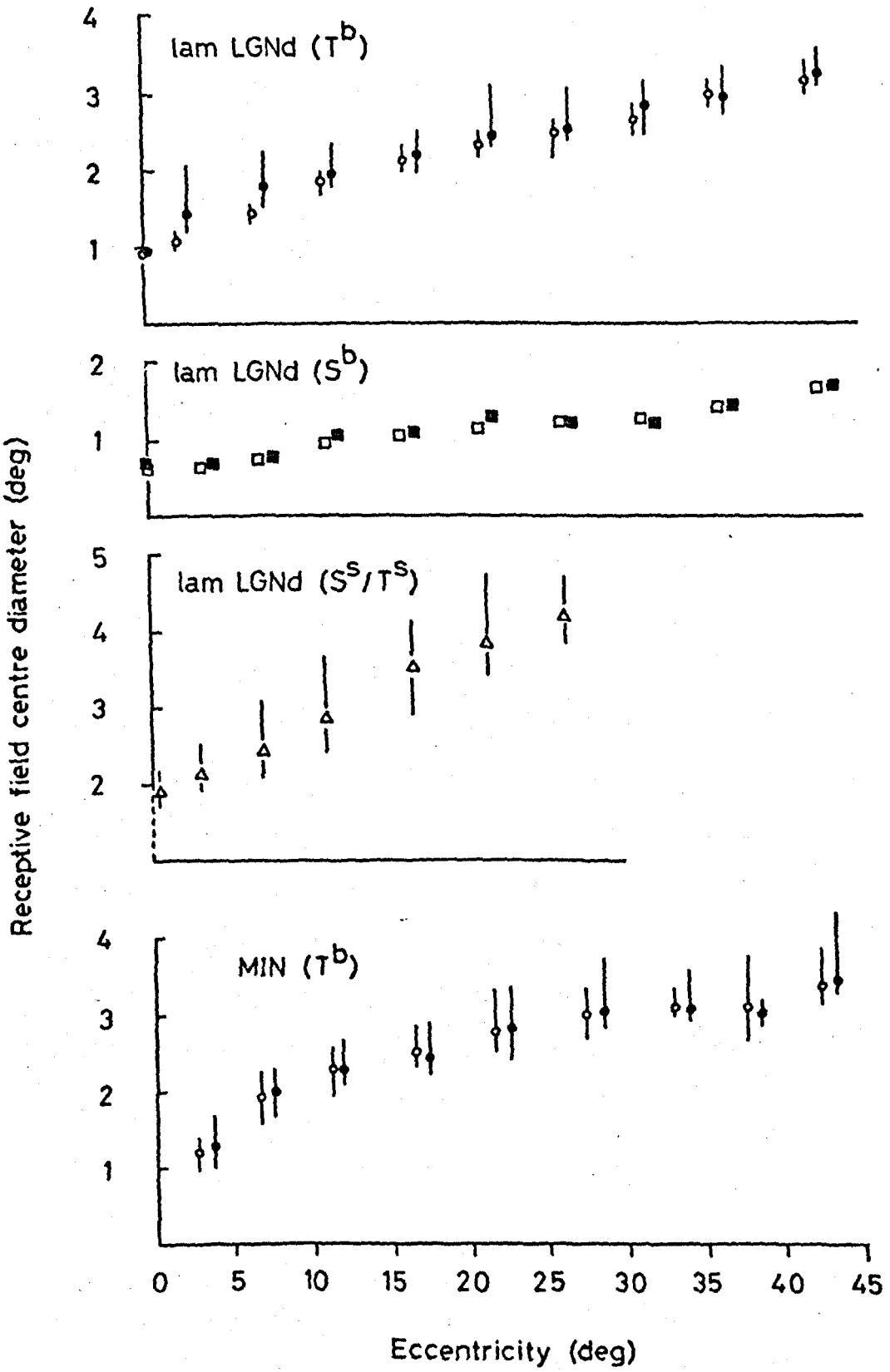
'Sluggish' cells also exhibited a preference for slowly moving stimuli (1-20°.sec^{-1}) and were rarely responsive to stimulus velocities exceeding 100°.sec^{-1} (Fig. 7). There was no apparent velocity preference shown by either sustained or transient types within the 'sluggish' class. In contrast, 'brisk' transient cells

responded relatively poorly at slower velocities but vigorously at faster ones (50-120°.sec^{-1} - Figs. 5 and 6), while 'brisk' sustained cells responded well over a range of velocities (1-100°.sec^{-1}), with a tendency for the velocity range to be related to the receptive field centre size, cells with smaller centres preferring slower velocities. A difference between the discharge of 'brisk' and 'sluggish' cells was generally noticeable over the audio-monitor, the 'brisk' cell response being crisper than that of 'sluggish' cells, reflecting the tighter spike clustering in the discharge of 'brisk' cells.

Cleland and Levick (1974a) described a 'twirling stimulus test' for distinguishing 'brisk' from 'sluggish' cells. This consisted of spinning a disc, having one surface black and the other white mounted on a wire, in the receptive field between 10-30 rev/sec. These authors claimed that the average discharge rate of 'brisk' transient cells could be driven above 120 spikes/sec; 'sluggish' transient cells in contrast were rarely driven above 75 spikes/sec. The success achieved with this stimulus during the study was poor. In order to overcome any deficiencies on the part of the experimenter a refinement of the test was used. Similar intermittent stimulation was achieved on the CRT display by rapid contrast reversal (i.e. white-to-black flicker on a 'grey' background) of a spot (1-2° diameter) centred over the receptive field. The response to such flicker stimulation resembled that of the twirl test in that 'brisk' transient cell mean discharge was driven above 100 spikes sec^{-1}, (Figs. 5 and 6), compared with 50-80 spikes sec^{-1} for 'sluggish' transient cells (Fig. 7), at the optimal flicker frequency. This further revealed a distinction between 'brisk' sustained and transient cell types, whereby the flicker

Fig. 8.

Receptive field centre sizes as a function of eccentricity (over ranges of 5°) from the area centralis of 'brisk' transient cells (T^b: circles), 'brisk' sustained cells (S^b: squares), and 'sluggish' sustained and transient cells (S^s/T^s: triangles) recorded from the laminated LGNd; 'brisk' transient cells (T^b: circles) recorded from the MIN. For the 'brisk' cells, open symbols represent off-centre, and filled symbols on-centre cells. Vertical bars through symbols represent range of sizes found.


lam LGNd (T^b)
lam LGNd (S^b)
lam LGNd (S^s/T^s)
MIN (T^b)
Receptive field centre diameter (deg)
Eccentricity (deg)
0
5
10
15
20
25
30
35
40
45

frequency-response curve for 'brisk' sustained cells (and for both 'sluggish' sustained and transient) tended to be horizontal (i.e. independent of flicker frequency - Fig. 4) while that for 'brisk' transient cells showed an inverted U function (i.e. response varies with flicker frequency - Fig. 5 and 6).

3.2.11. Periphery effect:

The periphery effect could not be elicited in either 'sluggish' sustained or transient cells, in contrast with the majority of 'brisk' transient cells.

3.2.12. Receptive field centre size:

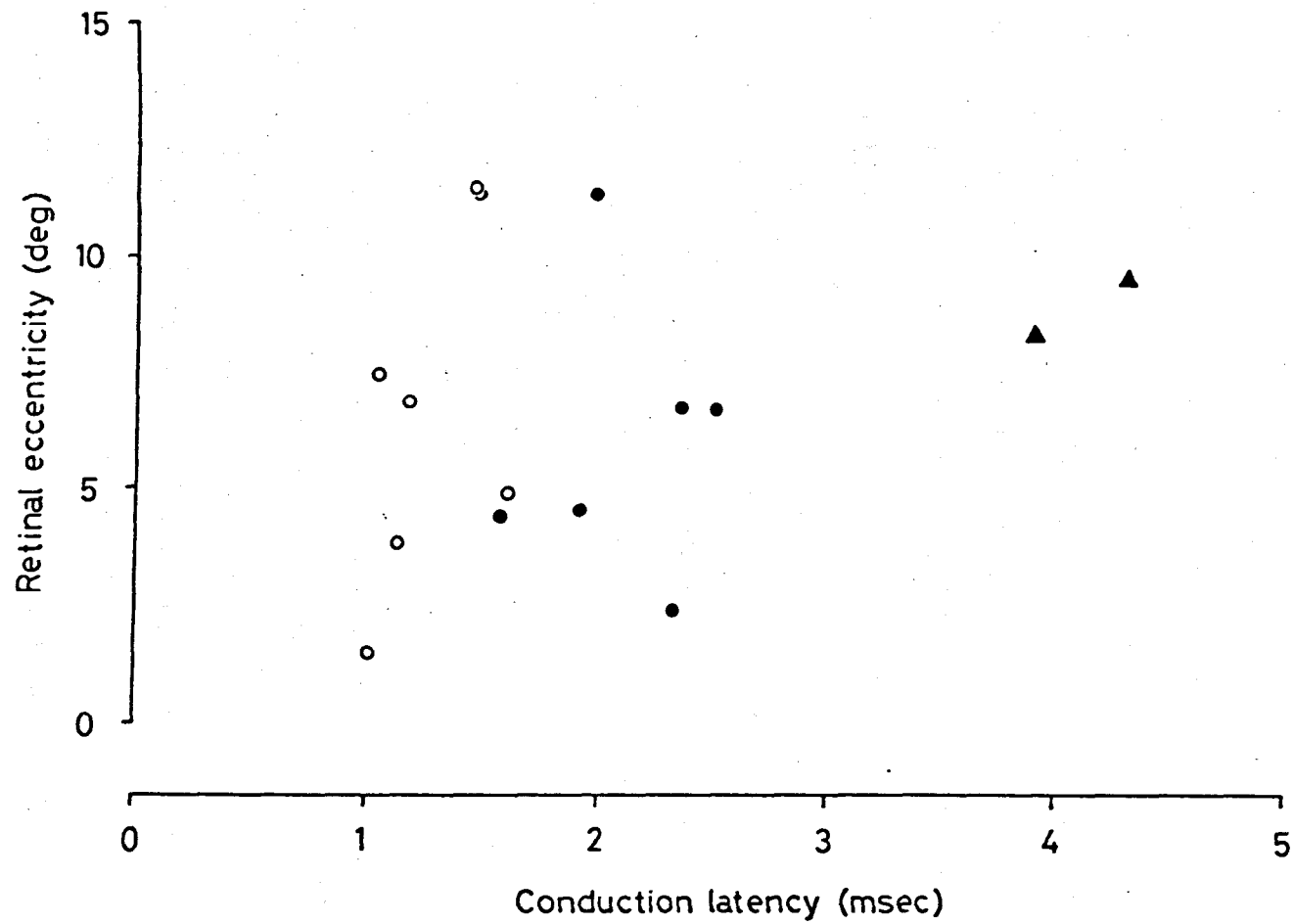
Receptive field centres were plotted as described earlier for 'brisk' cells, and were similarly elliptical or more rarely circular in shape. RFC sizes were found to be of similar dimensions for both 'sluggish' sustained and transient cells (2°-4° in diameter), and no correlation between RFC size and sustained/transient properties was apparent, which is in contrast with 'brisk' cell types (Fig. 8) where 'brisk' transient cells have larger receptive fields than sustained cells for a given retinal eccentricity. There was also a greater scatter in RFC sizes of on-centre and off-centre cells within either sustained or transient cell groups. As with 'brisk' cells receptive field centres increased with increasing retinal eccentricity (Fig. 8).

3.2.13. Orthodromic latency measurements:

An attempt was made to relate the latency of orthodromic activation of cells, following electrical stimulation at the optic

Fig. 9.

Conduction latencies (to optic chiasm stimulation) for fifteen cells as a function of eccentricity from the area centralis. Circles 'brisk' cell types; triangles 'sluggish' cell types; filled symbols sustained; open symbols transient.


15
10
5
0
Retinal eccentricity (deg)
0
1
2
3
4
5
Conduction latency (msec)

chiasm, to their receptive field type. In three animals, out of a total of 40 cells, combined latency measurements and receptive field properties were assessed in fifteen; the sample included eight 'brisk' transient cells (six from layers A, A_1 and C; and two from the MIN), five 'brisk' sustained cells (in layers A and A_1), and two 'sluggish' sustained cells (layer C). The latency range encountered in this small sample is similar to that reported by previous authors (Cleland et al, 1971b; Fukada & Saito, 1972; Hoffmann et al, 1972) in the case of 'brisk' transient and 'brisk' sustained cells with orthodromic latency ranges of 1.0-1.6 msec. and 1.5-2.5 msec respectively (Fig. 9). However the two 'sluggish' sustained cells had latency measures of 3.9 and 4.5 msecs. indicative of slow velocity fibres, approximately 4m. sec^{-1} (assuming a 12mm conduction distance from the optic chiasm), a measure similar to that of the slow afferent projection (W cells or 'sluggish' cells) to the midbrain (Fukuda & Stone, 1974; Cleland & Levick, 1974a). Although based on a small sample (15 cells) there was a correlation between orthodromic latency (hence conduction velocity) of a cell's input and that of the cell's receptive field type.

Further aspects of the sustained/transient classification, in particular with regard to receptive field organization and moving contours, will be dealt with in Chapter 4 when discussing responses of cells in the LGNd complex to textured stimuli. However, of those properties discussed so far, with the exception of a differential distribution of cell types (see sections 3.4), the only apparent differences between the 'brisk' transient cells found in the MIN and laminated LGNd were those of:

(a) receptive field centre size in that the 'brisk' transient cells recorded from the MIN tended to be larger than those recorded from the laminated LGNd (see Fig. 8).

(b) only rarely (10/231 cells) was there any tonic component in the response to standing contrast (even -N_2O/O_2 preparations) from 'brisk' transient cells recorded within the MIN compared with the laminated LGNd (see Figs. 5 and 6) which were similar in this respect to cells in the MIN with exception of 'brisk' transient cells recorded in the upper (magnocellular) portion of layer C (see later).

3.3. Other cell types:

Through application of the preceding tests it was possible to classify most of the cells recorded within the LGNd complex as sustained or transient, 'brisk' or 'sluggish'. For about 10% of cells it was difficult from just the response to standing contrast alone to classify cells as either sustained or transient; however, this figure is exaggerated owing to the fact that it includes cells classified before the 'brisk'/'sluggish' distinction was made. In such cases the other tests were relied upon and for nearly 7% of the total cell sample it was not possible to clearly differentiate them as sustained or transient for they possessed a mixture of sustained and transient properties - observations reported similarly by others (Cleland et al, 1971b; Hoffmann et al, 1972).

In addition to cells with mixed sustained/transient properties, other cell types were occasionally recorded which lacked the on-centre or off-centre concentric organization. Most of these (49/55) cells possessed on-off receptive fields which were generally circular

or oval in shape (two cells had elongated fields but this did not confer any orientational or directional properties). The on-off cells could be further classified as to their directional sensitivity and monocular or binocular drive.

3.3.1. On-Off cells (non-directional):

When mapped with a small (0.5°-1.0°), flashed exploratory spot, cells yielded transient responses at both stimulus onset and offset. The strength of the on and off responses for different positions of the spot was variably scattered throughout the receptive field.

Cells responded to both light and dark stimuli moving in any direction across their receptive fields. The response was found to decrease when the stimulus was increased in size beyond the receptive field perimeter suggesting some form of suppressive outer zone surrounding the on-off centre. A large, flashed spot encroaching into this 'suppressive zone' was also found to elicit a reduced response in comparison with that elicited by a smaller spot. Flashed annular stimuli tended to be ineffective unless their inner boundary overlapped the edge of the on-off field, when on/off responses comparable to that evoked by flashed spots were elicited.

Non-directional on-off cells could be further sub-classified according to their on-off receptive field size and whether or not they were binocularly driven. Monocularly driven cells (11) tended to have RF sizes of 2-3° in diameter while binocularly driven cells (35) were not only more numerous but had fields 4-8° in diameter (and only occasionally was a suppressive zone found to be present). The binocular on-off cells also had a different distribution within the LGNd complex (see section 3.4.). The monocular on-off cells

would appear to be equivalent to the 'local edge detectors' of Cleland & Levick (1974b) or 'excited-by-contrast' cells of Stone & Hoffmann (1972).

3.2.2. On-Off cells (directional):

These cells (3) resembled the monocular on-off cells described above with the exception that they exhibited a preferred direction of motion. Cells tended to be unresponsive at velocities above $50°.sec^{-1}$ and, as with non-directional cells, responsiveness declined with increased stimulus dimensions, suggesting a suppressive surround zone. The on-off responses mapped within the receptive field provided no clue to the directional preference of the cell.

3.3.3. 'Suppressed-by-contrast':

Four such cells were recorded and were characterized by a relatively high maintained firing rate (15-30 $spikes.sec^{-1}$) which was suppressed at the onset or offset of a flashed spot over the receptive field, or by a moving spot or bar of either contrast, moving across the receptive field. These cells are similar to those initially described by Rodieck (1967) and later by others (Stone & Hoffmann, 1972; Cleland & Levick, 1974b).

3.3.4. Off-centre, on-off surround:

Two other cells, from layer C_1, had properties which seemed to be different from cells reported in the literature. Flashed stimuli revealed an off-centre (about 6° diameter) and an on-off surround extending up to 15° across. Motion of stimuli confined within the off-centre evoked only an initial phasic discharge, and subsequent

movement has no further effect, whereas discontinuous motion of stimuli confined to the on-off surround evoked a phasic discharge to each movement.

3.3.5. Unit recordings from fibres:

The receptive field properties of a further 28 units, judged to be fibre recordings on the criteria of Bishop et al (1962a,b), were examined.

Many of these units were probably either optic radiation (11) or optic tract fibres (12). These were distingusihable by the higher maintained discharge rate of optic tract fibres and lack of any clustered spontaneous spikes such as occur in LGNd cells (radiation fibres), particularly in pentobarbitone preparations. Sustained and transient cell distinctions were also clearer for presumed optic tract fibres.

The five remaining fibre recordings had receptive fields which resembled those of complex cells of the striate cortex and were regarded as being cortico-fugal fibres.

There was a tendency for such fibre recordings to be isolated with pipettes of higher impedance and smaller tip diameter.

3.4.

Distribution of receptive field types in the LGNd complex:

While sustained and transient cells have been described in the laminated LGNd (Cleland et al, 1971b; Hoffmann et al, 1972) the distribution of cell types between the various laminae has only been briefly commented upon - "transient and sustained cells were found in all three layers of the LGN" (Cleland et al, 1971b).

With regard to the MIN, previous electrophysiological studies have been primarily concerned with visual field mapping (Kinston et al, 1969; Sanderson, 1971) and only on-centre and off-centre receptive fields have so far been described. During the course of the present study there have been independent reports that the majority of cells within the MIN are of the transient (Y) type (Dreher & Sefton, 1975; Palmer et al, 1975) in agreement with the author (Mason, 1975).

The present results provide data for a differential distribution of 'brisk' and 'sluggish', and sustained and transient cell types within the laminated LGNd and MIN. The results also supplement other anatomical and electrophysiological demonstrations of laminar organization of crossed and uncrossed retinal afferents in laminated LGNd, and evidence of laminar organization in the MIN.

The results will be presented as two studies: 'LGNd - complex study I', which comprises that cell sample accumulated during earlier investigations when no distinction between 'brisk' and 'sluggish' types was made (Table 1); and 'LGNd-complex study II' when such distinctions were made (Table 2).

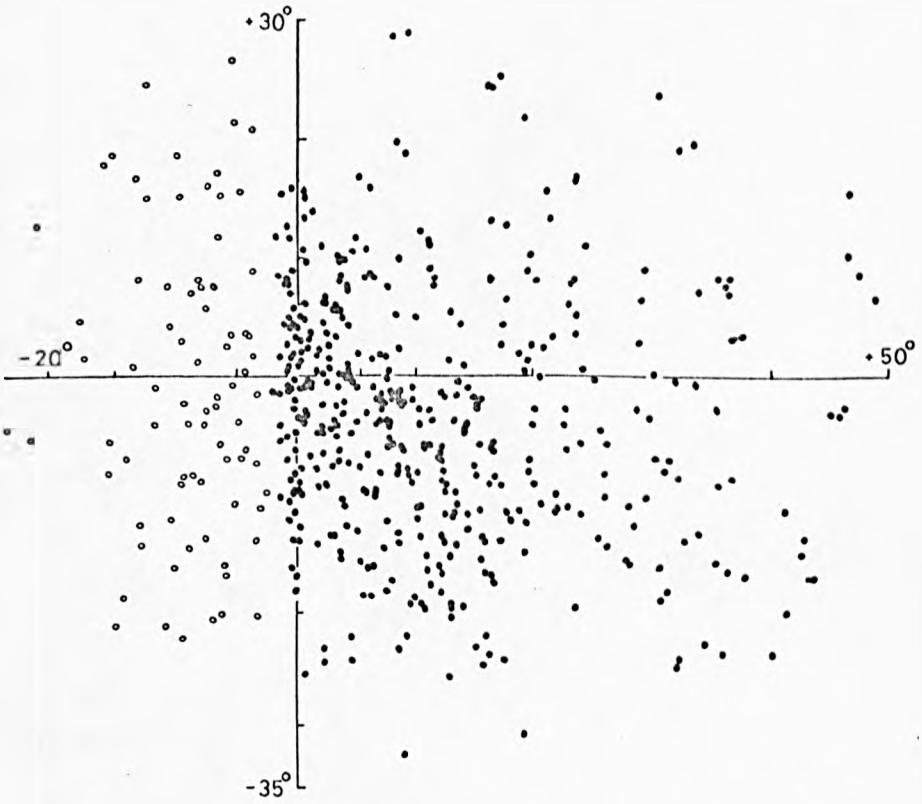
3.4.1. Laminar organization in laminated LGNd:

Guillery (1970), in an anatomical study, has described five layers in the laminated LGNd; layers A and C receive contralateral retinal afferents; layers A_1 and C_1 receive ipsilateral afferents; and layer C_2 receives none. This laminar organization has been confirmed electrophysiologically (Daw & Pearlman, 1970; Sanderson, 1971; Guillery & Kaas, 1971). More recently, Hickey and Guillery (1974) reported that layer C_2 was further divisible into C_2 (receiving contralateral input) and C_3 (receiving no retinal input).

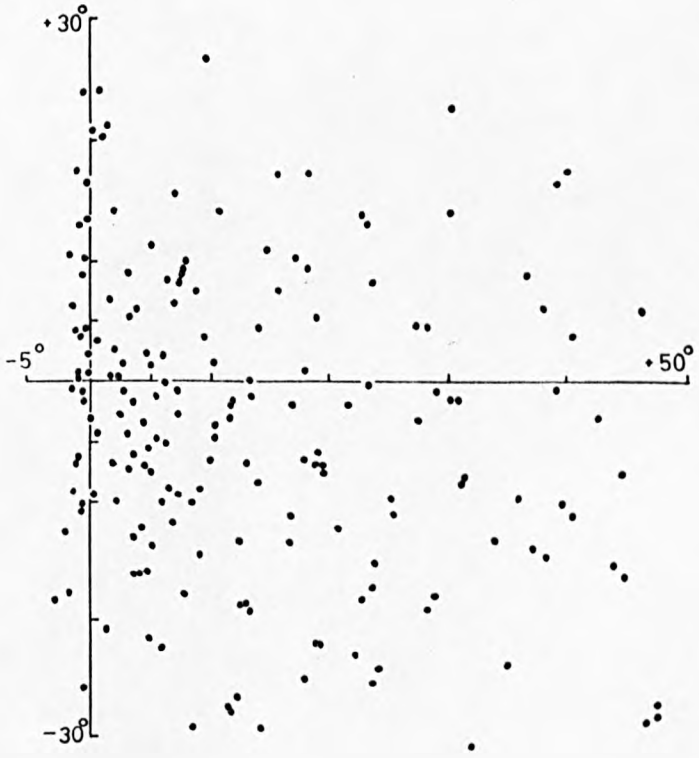
Fig. 10.

Distribution in the visual field of the receptive field centre points of cells recorded from the laminated LGNd and MIN. The open circles in the ipsilateral visual field exhibiting large nasotemporal overlap in the LGNd distribution are from LGNd studies I and II and constitute the cells considered to be from the medial limb of layer C.

laminated LGNd



MIN:



A total of 476 cells (from LGNd studies I and II, but excluding the cells isolated in the medial limb of layer C during study I) were located in the laminated LGNd and their distribution within the laminated LGNd is tabulated in Tables 1 and 2; (receptive field distribution in the visual field is depicted in Fig. 10). When the locations of cells were compared with histological outlines of the LGNd there was a good correlation between the electrophysiological observation of driving eye with the appropriate layer. Thus, contralaterally driven cells were found in layers A and C, and ipsilaterally driven cells in layers A_1 and C_1. In addition, in some preparations a few (4) contralaterally driven cells (unclassified) were recorded ventral to ipsilaterally driven cells of C_1 and were located adjacent to the optic tract. This suggests such cells may constitute layer C_2.

Approximately 1 (6/476) of the total population of cells recorded in the LGNd complex were binocularly driven, possessing on-off receptive fields as described in section 3.3.1. These cells were found in the vicinity of the interlaminar zones between layers A and A_1, A_1 and C, which is in common with other electrophysiological studies.

Another property exhibited by geniculate cells located at the border of the laminated LGNd and MIN is nasotemporal overlap, i.e. some cells have receptive field centres which are across the vertical midline in the 'wrong' (ipsilateral) visual field. As described by Sanderson and Sherman (1972), two different populations of cells exist which were characterized by the extent of nasotemporal overlap they possess. Nasotemporal overlap in layers A and A_1 was found to overlap the vertical meridian up to 2.5° (i.e. measured to the centre

of the receptive field), with a mean of 1.5°, whereas cells in layer C possessed a nasotemporal overlap up to 23°, with a mean of 6.0°. Cells found to exhibit a nasotemporal overlap up to 2° in layers A, A_1 or C were either sustained or transient; while virtually all cells with larger nasotemporal overlap were ('brisk') transient.

3.4.2. Laminar organization in the MIN:

A total of 231 cells (including all the cells in the medial limb of layer C from study I) were recorded in the MIN of which 133 were contralaterally driven and 98 ipsilaterally driven; the distribution of receptive fields in the visual field is shown in Fig. 9. Hayhow (1958) has suggested that the MIN provides an example of 'concealed lamination' in that lamination is only detectable in degeneration studies.

Oblique electrode penetrations were used to investigate this 'concealed lamination' within the MIN, as previous studies employing vertical penetrations (Kinston et al, 1969; Sanderson, 1971) found no evidence for the trilaminar organization suggested by Hayhow (1958).

As described in previous electrophysiological mapping studies, the MIN was found to contain a mirror image of the representation of the visual field in the laminated LGNd in agreement with the detailed visual field projection maps of Sanderson (1971). There was a much greater range and rate of change of azimuth and elevation for cells in the MIN compared with those in the laminated LGNd. This reflects the condensation of the visual field representation into a volume of nervous tissue 1/5 - 1/6 that of the laminated LGNd. The central visual field was found to be represented at the middle of the antero-posterior extent of the MIN at its lateral border with the

the laminated LGNd, particularly the more dorsal aspects. Conversely, the peripheral visual field (up to about 45° was represented along the ventromedial edge of the MIN, adjacent to the inferior pulvinar.

With both vertical and oblique electrode penetrations, contralaterally and ipsilaterally driven cells tended to be recorded as clusters, although oblique penetrations revealed what appeared to be a partially overlapping arrangement of ipsilaterally and contralaterally driven cells (Fig. 11). This contralateral/ ipsilateral arrangement was interpreted as follows:

(i) a contralaterally driven group of cells located at the laminated LGNd - MIN border, a region in which it is particularly difficult to define the border between the MIN and layer C. The majority of these cells (32/52 - study I) were found to be of the transient type (in study II these cells were all included within layer C and of the 'brisk' type - see section 3.5.3) and exhibit large nasotemporal overlap (in general 3-15°, occasionally up to 26°).

(ii) an ipsilaterally driven group of cells occupying a central location within the MIN, which were almost exclusively transient cells (71/73), of the 'brisk' type (study II) nasotemporal overlap; was comparable to that of A-laminae cells (less than 2.5°).

(iii) a further contralaterally driven group of cells located along the medial and dorso-lateral edge of the MIN, all with 'brisk' transient properties.

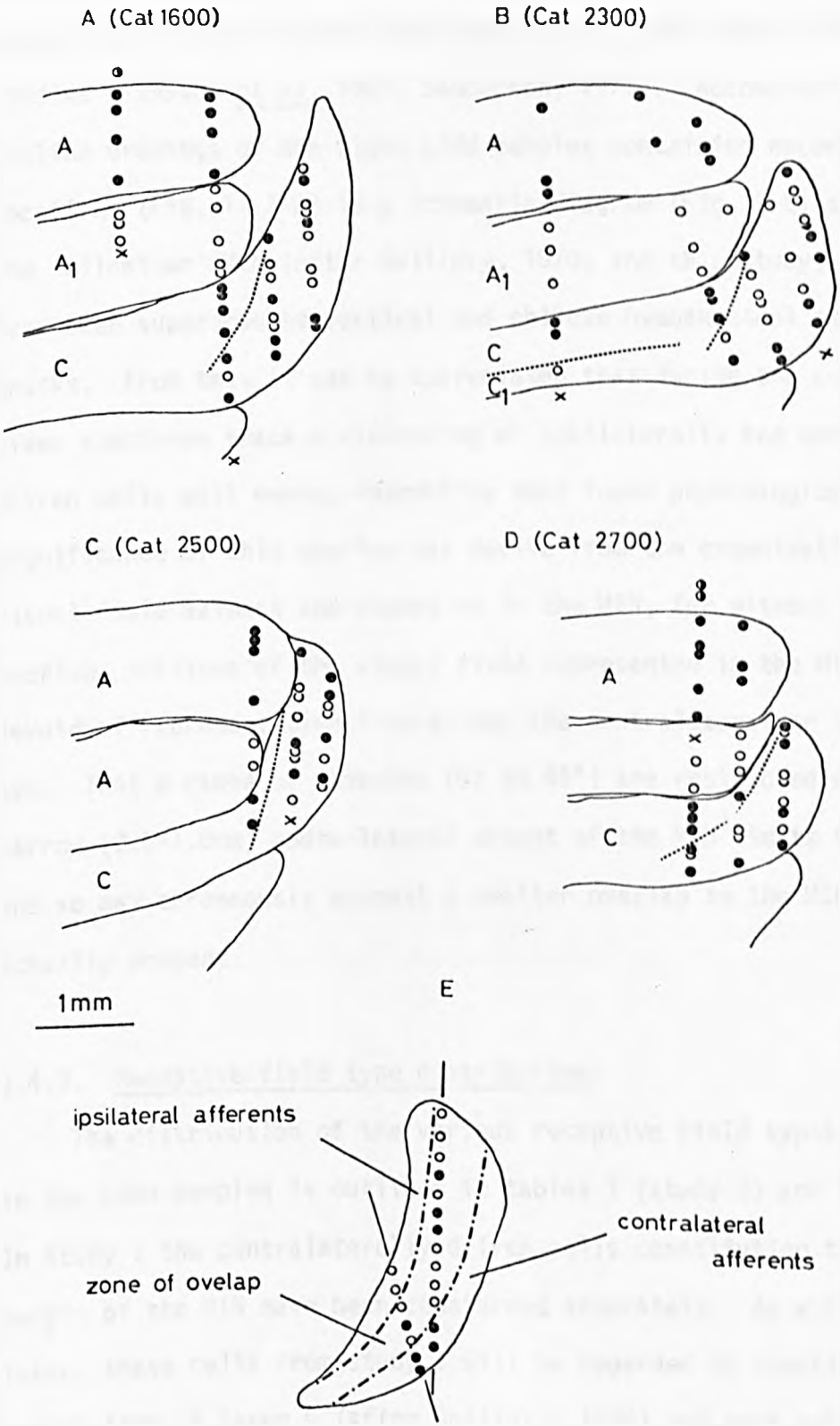
The extent of overlap between these contralaterally and ipsilaterally driven cell groups was found to vary between animals,

Fig. 11.

A-D: Outline drawings of the right LGNd complex with the locations of recorded cells for four experiments.

E: The 'bilaminar' MIN as a schematic diagram showing the presence of retinal afferent overlap (Also, not shown, there is some overlap between the ipsilateral afferent layer and the contralaterally driven cells of the medial limb of layer C) - see text.

Filled circles, contralaterally driven cells; open circles ipsilaterally driven cells. The dotted line in A-D indicates the electrophysiologically determined border of the 'bilaminar' MIN.


A (Cat 1600)
B (Cat 2300)
A
A1
C
A
A1
C
C1
C (Cat 2500)
D (Cat 2700)
A
A
C
A
C
1mm
E
ipsilateral afferents
contralateral
afferents
zone of ovelap

see Fig. 11. This probably reflects the extent of overlap of contralateral and ipsilateral retinal afferents in the MIN, as revealed following eye enucleation (e.g. Hayhow, 1958), and may account for the clustering found during this and other physiological studies (Kinston et al, 1969; Sanderson, 1971). Accompanying the outline drawings of the right LGNd complex containing recorded cell locations (Fig. 11 A-D) is a schematic diagram (Fig. 11E) showing the 'bilaminar' MIN (after Guillery, 1970; and this study), onto which have been superimposed vertical and oblique hypothetical electrode tracks. From this it can be appreciated that during the course of a given electrode track a clustering of ipsilaterally and contralaterally driven cells will ensue, resembling that found physiologically. The significance of this overlap may derive from the organization of visual field azimuth and elevation in the MIN, for without such overlap, portions of the visual field represented in the MIN would be devoid of representation from either the contralateral or ipsilateral eye. That a range of azimuths (up to 45°) are restricted within the narrow (0.5-1.0mm) medio-lateral extent of the MIN limits the sampling and so may erroneously suggest a smaller overlap in the MIN than actually present.

3.4.3. Receptive field type distribution:

The distribution of the various receptive field types encountered in the LGNd complex is outlined in tables 1 (study I) and 2 (study II). In study I the contralaterally driven cells constituting the lateral margin of the MIN have been considered separately. As will be argued later, these cells from study I will be regarded as constituting the medial limb of layer C (after Guillery, 1970) and such cells recorded

Table 1: LGNd complex study I

	layers A/A_1	layer C	layer C_1	layer C (medial limb)	MIN
sustained	67	26	9	19	—
transient	62	31	4	32	101
mixed	9	2	—	—	2
others	4^{+1}	5	4	—	—
unclassified	3	3	4	1	2
	145	67	21	52	105

Table 2: LGNd complex study II

	layers A/A_1	layer C	layer C_1	layer C_2	MIN
brisk sustained	61	7	—	—	—
brisk transient	49	43	—	—	71
mixed (brisk)	9	—	—	—	—
sluggish sustained	—	18	16	—	—
sluggish transient	—	5	4	—	—
others	2^{+1}	5	6	—	—
unclassified	3	5	6	4	3
	124	83	32	4	74

during study II have been included in the layer C sample.

Many experiments were directed at the organization of the C-layers and, in these, layers A and A_1 were often bypassed. The numbers of cells in the C-laminae (tables 1 and 2) is biased accordingly.

Tables 1 and 2 indicate a clear difference in the distribution of (a) 'brisk' sustained and transient cells within the laminated LGNd and MIN; (b) 'sluggish' sustained and transient cells within the laminated LGNd; and (c) cell types within layer C which although concealed in the results of Tables 1 and 2, has much significance with regard to neuronal organization in the MIN.

From the total of 154 MIN cells (study I) it is evident that the proportion of transient cells isolated within the MIN (86% overall) is higher than in the laminated LGNd (42%) - study I. This becomes more significant when it is realized that those sustained cells present in the MIN were not only all encountered at the lateral margin, bordering the laminated LGNd but were also contralaterally driven. Thus, excluding this lateral marginal region increases the proportion of transient cells in the remaining portion of the MIN to 96% (study I). Prior to the sub-classification of cells into 'brisk' and 'sluggish' types the available evidence from study I suggested that the lateral margin of the MIN could be regarded as an extension of layer C. This was argued from the facts that this group of cells resembled layer C in being contralaterally driven, exhibiting a large nasotemporal overlap (more than 3°) and in having a similar distribution of sustained and transient cells (37%: 61% compared to 45%: 54% sustained: transient respectively), representing a similar area of the visual field. These results are compatible with

Guillery's (1970) re-evaluation of earlier anatomical data (see Chapter 1) in which he regards the lateral margin of the MIN as the medial limb of layer C of laminated LGNd. This evidence is consistent with the MIN being a bi-laminar structure within which virtually all cells have transient properties. During study II this group of cells was therefore regarded as constituting the medial limb of layer C and thus excluded from the MIN sample. From a sample of 74 cells in study II, all of the classified cells (96%) were of the 'brisk' transient type.

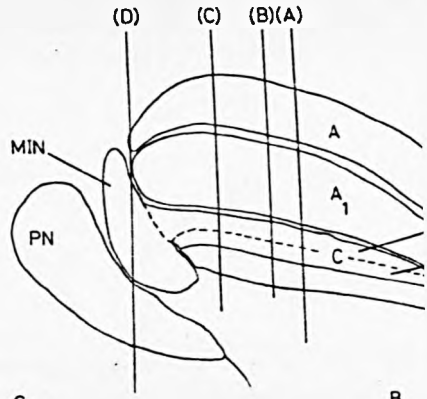
Also evident from table 2 is the differential distribution of 'brisk' and 'sluggish' cell types within the laminated LGNd, where almost all 'sluggish' cells appear to be contained within the C-laminae. However, within layer C itself there was evidence of a differential distribution of receptive field types - see Figs. 12 and 13 - which is concealed in the tabulated results. It was found that virtually all 'brisk' transient cells (88%) were located in the upper (magnocellular) portion of layer C, while 'brisk' sustained cells tended to be found throughout layer C, and the majority of 'sluggish' cells (65%) occupied the lower (parvocellular) portion of layer C. These observations from study II are presented in histogram form in Fig. 12.

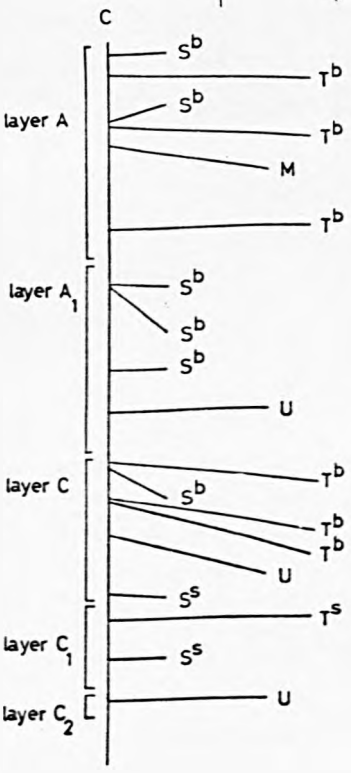
It is of interest to note that the magnocellular regions within the LGNd complex (i.e. the MIN and upper portion of layer C) have predominately 'brisk' transient cells while the parvocellular regions (layer C_1 and the lower portion of layer C) have 'sluggish' cell types. This relationship between cell somata size and receptive field type is comparable with the correlation between receptive field type and cell morphology in the cat's retina (see Chapter 1).

Fig. 12.

Outline drawing of the LGNd complex from Cat 3900 showing four electrode penetrations (A-D) and below is presented the distribution of receptive field types recorded during three (A-C) of the electrode tracks; the fourth electrode track entered the MIN and all cells recorded were of the 'brisk' transient type.

CAT 3900


(D)
(C)
(B)(A)
MIN
PN
A
A1
C


C
layer A
layer A1
layer C
layer C1
layer C2
Sb
Tb
M
U
Ss
Ts


B

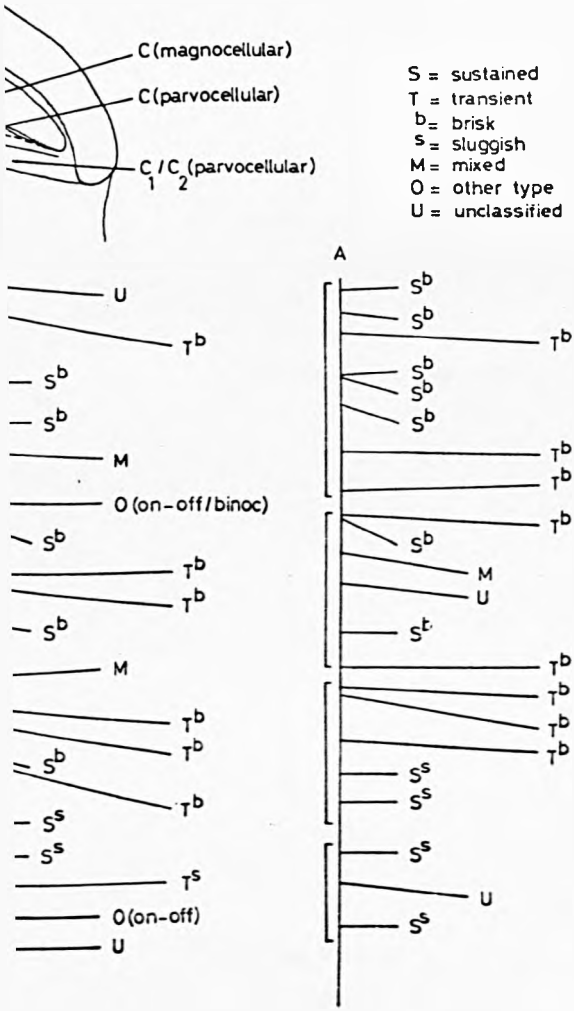
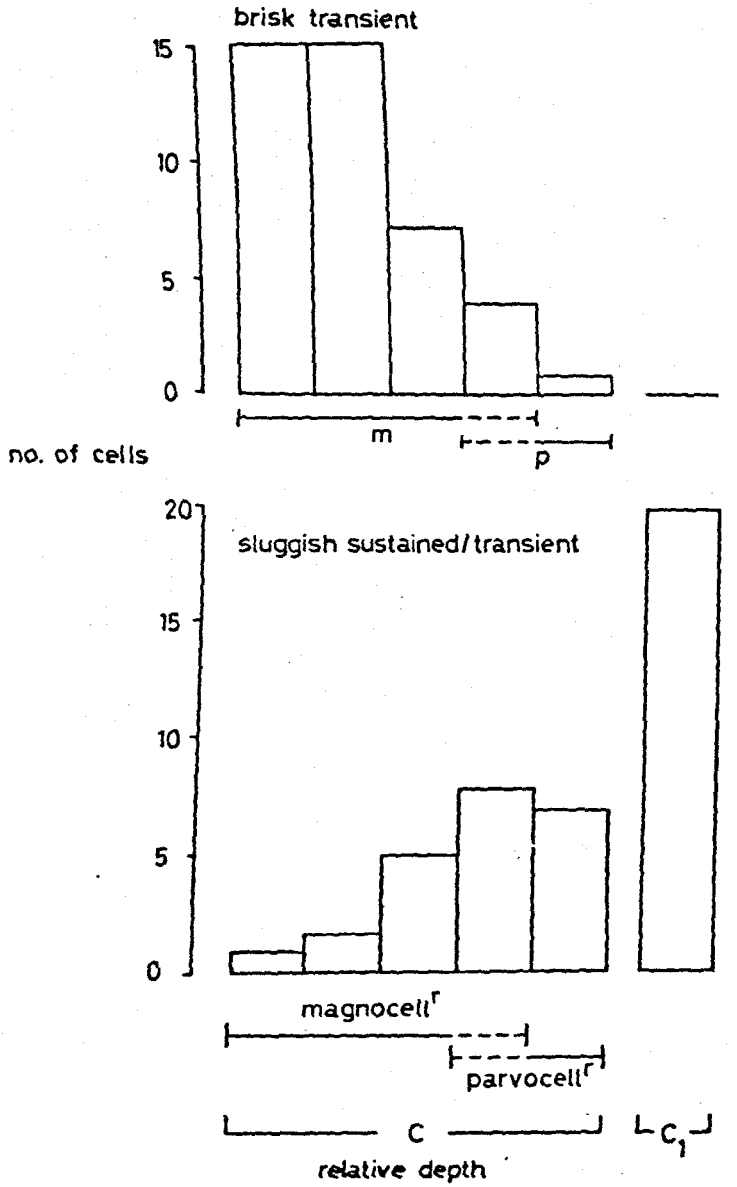
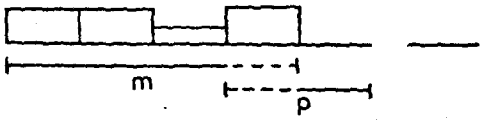

1mm
C (magnocellular)
C (parvocellular)
C1/C2 (parvocellular)
S = sustained
T = transient
b = brisk
s = sluggish
M = mixed
O = other type
U = unclassified
A
U
Tb
Sb
Sb
M
O (on-off/binoc)
Sb
Tb
Tb
Sb
M
Tb
Tb
Sb
Tb
Ss
Ss
Ts
O (on-off)
U
Sb
Sb
Tb
Sb
Sb
Sb
Tb
Tb
Tb
Sb
M
U
Sb
Tb
Tb
Tb
Tb
Ss
Ss
Ss
U
Ss

Fig. 13.

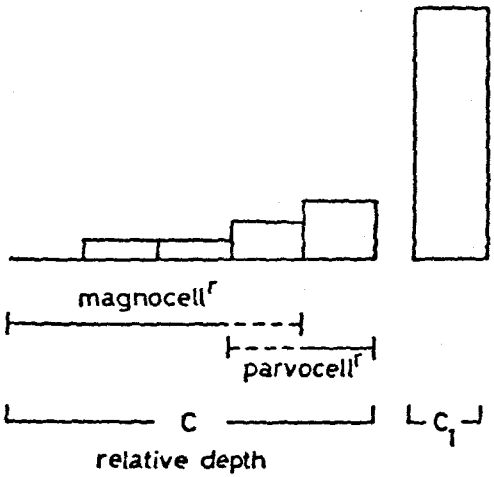
Distribution of 'brisk', 'sluggish', sustained and transient cells recorded from the C-layers during study II.


brisk transient
15
10
5
0
m
p
no. of cells
20
sluggish sustained/transient
15
10
5
0
magnocell^r
parvocell^r
C
C_1
relative depth

brisk sustained



unclassified / other types



It was with this background that orthodromic latency measurements following electrical stimulation at the optic chiasm were undertaken. As described in section 3.4., there appeared to be a relation between latency (hence conduction velocity) and cell type recorded in the LGNd complex. Within layer C the shortest latencies were recorded in the upper (magnocellular) portion and the longest latencies in the lower (parvocellular) portion, reflecting the distribution of receptive field types. Thus, for cells in the LGNd complex, as in the retina, a relationship between cell function and morphology appears to be present. Further, a relay of 'sluggish'/W-cell information through the geniculate to the visual cortex has been suggested (Cleland et al, 1975, 1976; Wilson & Stone, 1975; present study). Previous authors concluded that such information was exclusively projected to the midbrain visual system (Stone & Fukuda, 1974).

There was also a differential distribution in the LGNd complex of the on-off classes of cells. All of the monocular class (16) were recorded in layers C (parvocellular) and C_1 while the binocular cells (6) were confined to the interlaminar regions between layers A and A_1, and A_1 and C. Binocular on-off cells (29) were also commonly recorded just above the laminated LGNd, a region corresponding to the perigeniculate nucleus (NPG), in common with Sanderson (1971). The 'suppressed-by-contrast' and off-centre, on-off surround cells were also found to be located in the parvocellular portion of the C-layers.

The demonstration of a differential distribution of cell types within layer C of laminated LGNd has a significant bearing on the interpretation of organization within the MIN. The population of

'brisk' transient cells in the upper, magnocellular portion of layer C corresponds to previous anatomical descriptions of the magnocellular, central interlaminar nucleus (CIN) of Thuma (1928) - equivalent to the lamina magnocellularis of Rioch (1929) and lamina III per centralis of Kanaseki (1958) - and regarded as the dorsal margin of layer C by Guillery (1970) - see Fig. 1.

In histological section, the magnocellular portion of layer C and the lateral margin of the MIN (the medial limb of layer C according to Guillery) appears to be continuous. These two regions, between them, contain a complete representation of the contralateral visual field (mapped in similar fashion to the A-laminae), the medial portion of which has cells whose receptive fields exhibit a considerable nasotemporal overlap. The majority of cells within these regions have 'brisk' transient properties. This evidence warrants that the CIN be redefined as comprising the magnocellular portion of layer C and lateral margin of the MIN, which differs from anatomical descriptions only in its inclusion of the contralaterally driven cells along the lateral edge of the MIN. This description of the CIN should not be confused with the erroneous description of the 'dorsal CIN' and 'ventral CIN' which lie in the interlaminar regions, i.e. between layers A and A_1, and A_1 and C, by many authors (e.g. Kinston et al, 1969). Guillery (1970) has referred to these scantly cellular regions as the interlaminar plexi. It is in these regions that binocularly driven cells were recorded during this study.

3.5.

Organization of LGNd complex projections to areas 17 and 18:

The similarity between the MIN and the CIN, with respect to their 'brisk' transient cell populations, leads to the notion that these cell groups be regarded as a magnocellular entity (homologous with the magnocellular layers in other species) which has differentiated in the cat (and in other species), the 'bilaminar' MIN having 'flipped' through 180° to mirror the 'unilaminar' CIN. This description, argued from physiological evidence, supports Thuma's (1928) histological thesis that the MIN is a differentiated portion of the CIN. This raises the question of the possible functional significance of this differentiated organization, particularly in view of the present study which indicates little, if any, difference in receptive field properties between cells in the MIN and CIN. That this histological differentiation might reflect a differential cortical projection from the LGNd complex seemed a possibility, particularly as Tretter and colleagues (1975) suggested that area 18 of the cat's visual cortex should be regarded as a primary, rather than a secondary, visual area, being organized in parallel with area 17. Many anatomical studies have demonstrated that the projections from the MIN are extrastriate, while those of the CIN have been less widely studied - see Chapter 1.

In order to investigate the possibility of a differential projection, tracing of retrograde HRP transport from injection sites in areas 17 and 18 was attempted in four experiments. For three experiments, no HRP-positive cells were found in the LGNd complex, despite the fact that the HRP was successfully ejected from the micropipette as judged by the positive identification of extracellular

histochemical reaction product at the injection site. In the fourth experiment (cat 4900) a different grade of HRP was used (Sigma Type VI) to that of the previous experiments (Sigma Type II - single batch), which resulted in the identification of HRP-positive cells in the LGNd complex (Fig. 14).

Cat 4900:

To be confident that the injection sites were in areas 17 (V I) and 18 (V II), an oblique approach was used. In the case of the area 17 injection the pipette was directed lateromedially, entering the right hemisphere at A 2, RL 2. That receptive fields of recorded cells shifted progressively more peripherally with increasing penetration depth suggested that the pipette was in V I, and an appropriate injection of 4μA for 30 min. was then made (Fig. 14). The opposite (left) hemisphere was used for the area 18 (V II) ejection, the pipette being directed mediolaterally at °, entering the cortex at A2, LL4. The presence of larger response fields and progressive increase in azimuth indicated the pipette was in V II and an injection was then made (4μA for 30 min.) - Fig. 14. During the latter stages of the post-injection survival period (30 hours), penetrations were made over each LGNd complex with pontamine sky blue dye-filled micropipettes at co-ordinates appropriate to the mapping of the visual field corresponding to the HRP injection site in the cortex. This completed, the animal was perfused intra-arterially and histology carried out, as outlined in Chapter 2.

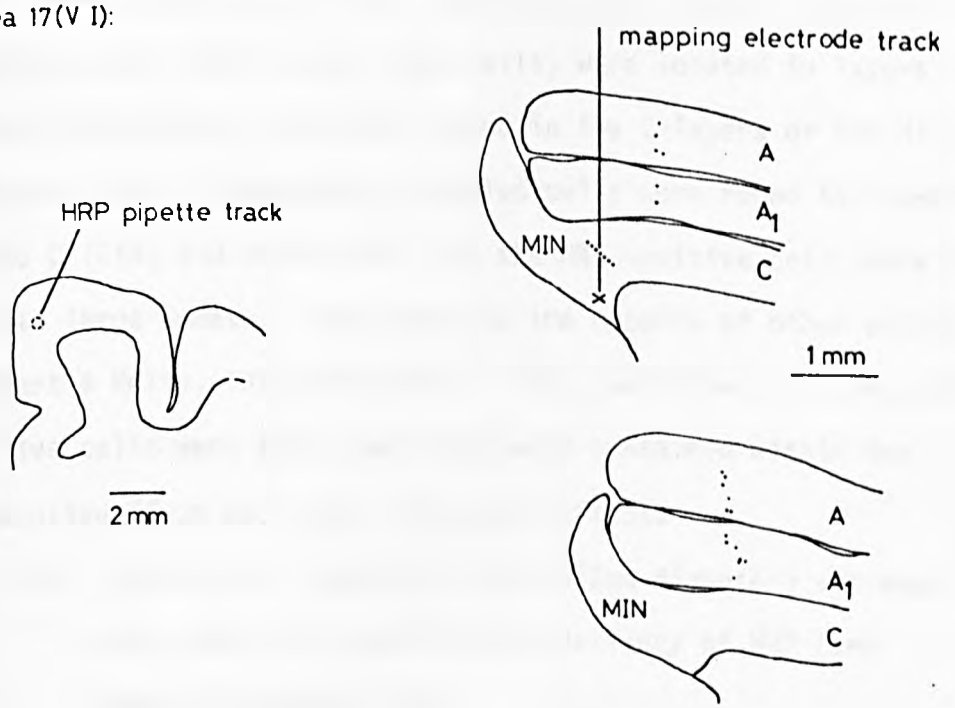
The results from this experiment are presented in Fig. 14, which shows the cortical injection sites and position of HRP-positive cells in the LGNd complex. It was considered safe to utilize both hemispheres in one animal as no projection from the LGNd to the

Fig. 14.

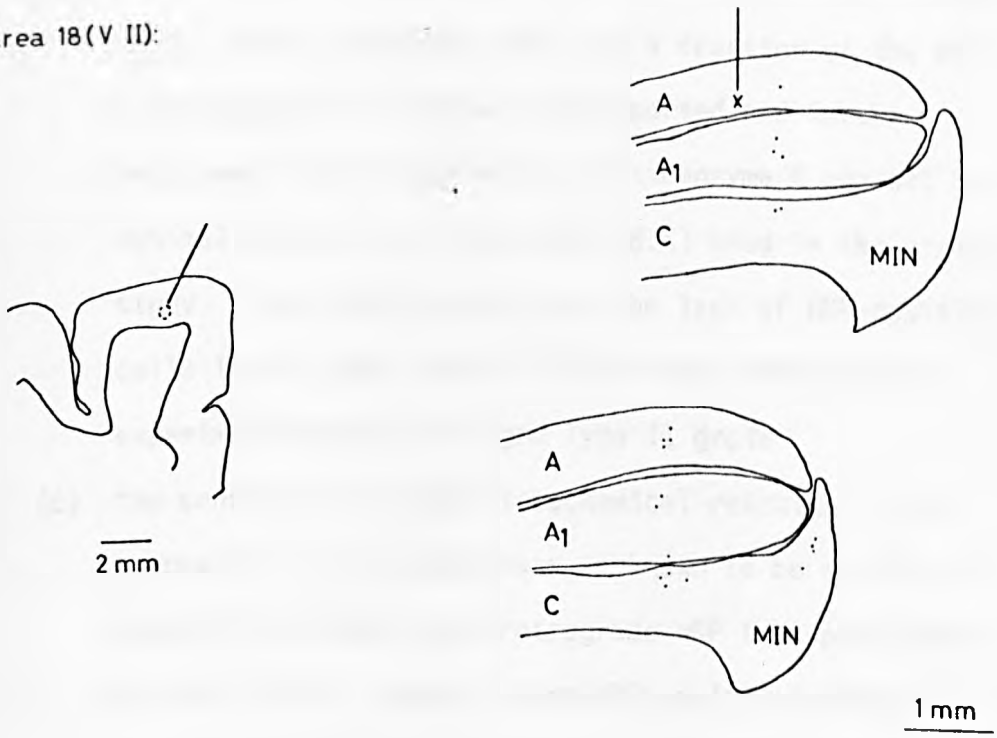
HRP retrograde tracing experiment (Cat 4900) showing the injection sites in area 17 (V I) of the right hemisphere and in area 18 (V II) of the left hemisphere, together with outline drawings of the LGNd complex showing the positions of HRP-positive cells (all of which were contained within two 50μ sections). The x at the end of the electrode tracks in the LGNd complex indicate positions of dye marks; the dotted line in layer C indicates the electrophysiologically determined border of the 'bilaminar' MIN.

Cat 4900:

Area 17(V I):



Area 18(V II):



contralateral cortex is reputed to be present (e.g. Burrows & Hayhow, 1971; Rosenquist et al, 1974). Following the area 17 injection, HRP-positive cells (medium and large cells) were located in layers A and A_1; no HRP-positive cells were found in the C-layers or the MIN. After the area 18 injection, labelled cells were found in layers A, A_1 and C (CIN) and in the MIN; all the HRP-positive cells were found to have large somata. Compared with the reports of other authors (Gilbert & Kelly, 1975; Maciewicz, 1975), relatively few (40) HRP-positive cells were found and these were contained within two consecutive 50 μm sections. This may reflect:

(a) the smaller injection sites (0.7mm diameter) achieved using the microiontopheretic delivery of HRP (see Graybiel & Devor, 1974)

(b) the inadequate transport of HRP. A recent report (Bunt et al, 1976) indicates that only a fraction of the HRP (iso-enzyme C) is actively transported and further cautioned that iontophoresis of isoenzyme C may not be optimal at the buffer pH level (8.6) used in the present study. This might account for the lack of HRP-positive cells in the LGNd complex in the three previous HRP experiments using the Sigma Type II grade

(c) the sensitivity of the histochemical reaction for the composition of the perfusate is known to be a critical factor in demonstrating retrograde HRP transport (Kim & Strich, 1976). However, more HRP-positive cells may have resulted if more successful experiments were available.

The location of these HRP-positive cells in the LGNd complex, with

regard to visual field representation (deduced from the mapping electrode penetrations and Sanderson's (1971) visual field map for the LGNd), are in accord with the cortical injection sites. Fewer labelled cells were located in the MIN (and the CIN) compared with the laminated portion (specifically layers A and A_1) of the LGNd, which probably reflects the condensed visual field representation present in the MIN and presumably, from these data, a more diffuse cortical projection field.

The results from this experiment suggest that the cortical projections from the MIN and the CIN are similar, with respect to their differential projections to area 18. These results are also compatible with previous reports that the axons of large cells in the laminated LGNd appear to bifurcate, projecting to areas 17 and 18, while medium-sized cells appear to project exclusively to area 17 (Garey & Powell, 1967). That no small cells were labelled may be attributed to various factors: some of these cells may be interneurones with no cortical projections; others may project to cortical areas outside area 18; or it may be an artefact of the histochemical technique. Nauta et al (1974) have cautioned that not all pathways may be revealed using the HRP technique.

During the course of these experiments, there were a number of reports of the laminar and cytological projections from the LGNd to areas 17 and 18 (Gilbert & Kelly, 1975; Maciewicz, 1975; Laemle, 1975) which extend the more limited findings of this present study. Laemle (1975) commented that the large cells in layer C contained no HRP label after area 17 injections, in agreement with the present study. Support for the similar differential cortical projection from the MIN and CIN and for the assertion that no cortical projection from

the interlaminar plexi (often erroneously referred to as the dorsal and ventral components of the CIN) is present, is provided by many authors (Burrows & Hayhow, 1971; Shoumura, 1973; Gilbert & Kelly, 1975).

That a differential projection from either the MIN or the CIN to extrastriate areas, other than area 18, may be present is suggested from Maciewicz's studies (1974, 1975). Maciewicz (1975) reported HRP labelled cells in the MIN and in the C-layers, following area 19 injections; however, whether the parvocellular and/or magnocellular portions are responsible for this projection cannot be resolved as Maciewicz made no mention of diameters of the labelled cells in the C-layers. A differential projection to the medial division of the CBA appears to be present for, following HRP injections in CBA, Maciewicz (1974) observed HRP-positive cells only in the MIN.

Chapter 4

LGNd COMPLEX. II: RESPONSES TO MOTION OF CONTRAST CONTOURS AND TEXTURED VISUAL STIMULI

Light and dark edges and bars have been used extensively in single-unit studies at various levels of the cat's visual system. However, in recent reports from this laboratory, Hammond and MacKay (1975a,b; 1976) have demonstrated that simple and complex cells in the cat's striate cortex are differentially sensitive to motion of textured 'visual noise'. An investigation of the responses of cells in the LGNd complex was undertaken (the cell sample being drawn from LGNd study II of the previous chapter) to determine whether or not a similar differentiation of cell types was possible using textured visual noise, with the further possibility in mind that it might provide additional clues to the neuronal organization within the constituent nuclei of the LGNd complex.

The responses of different classes of cells to conventional light or dark bar stimuli were compared with those to textured visual noise.

4.1. Response patterns to moving contrast bars:

'Brisk'/'sluggish' sustained and transient cells were further characterized as either 'centre-activated' or 'centre-suppressed', depending on the contrast of the moving stimulus bar used and whether the cell was an on-centre or off-centre type. Thus, for on-centre cells, light bars evoked centre-activated responses and dark bars centre-suppressed responses. The converse was true for off-centre

cells. These results are similar to those initially reported by Rodieck and co-workers (Rodieck, 1965; Rodieck & Stone, 1965; Kozak et al, 1965) for concentrically organized receptive fields of retinal ganglion and lateral geniculate cells, prior to their differentiation into 'brisk'/'sluggish', sustained or transient types.

In the following description of response types a * indicates centre response of the cell either centre activation ($\overset{*}{E}$) or centre suppression ($\overset{*}{I}$). The initials E and I also signify the activation and suppression, respectively, of sequential components in the response pattern. A schematic diagram of the various response patterns (as PSTH's) found are shown in Fig. 15 and actual examples in later figures.

4.1.1. On-centre cells:

Three types of centre-activated response patterns were evoked by moving narrow light bars (i.e. bar widths less than the receptive field centre diameter).

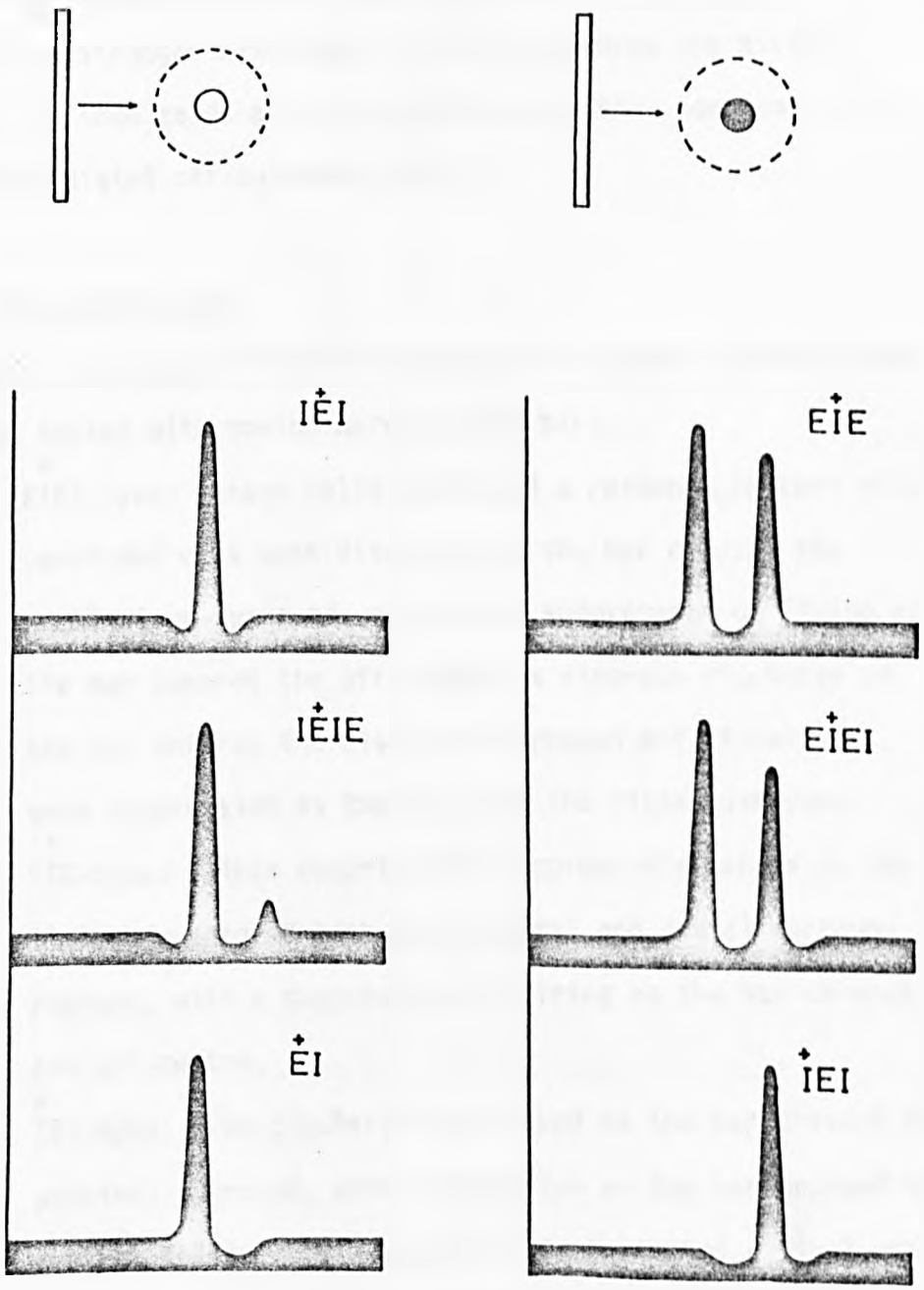
(i) $I\overset{*}{E}I$-type: this consisted of a suppression of firing as the bar entered the proximal and distal off-surround regions of the receptive field separated by a vigorous discharge as the bar entered the receptive field centre.

(ii) $I\overset{*}{E}IE$-type: these cells responded in essentially similar manner to those of the $I\overset{*}{E}I$-type but, in addition, exhibited a further discharge as the bar left the distal surround.

(iii) $\overset{*}{E}I$-type: these cells only yielded a double component response to motion of a light bar and lacked any suppression of firing as the bar entered the proximal surround.

Fig. 15.

A schematic diagram of the various response patterns of LGN cells to motion (in PSTH format) found (after Rodieck & Stone, 1965) - see text.



Centre-activated

Centre-suppressed

When tested with dark bars, most cells yielded a triple component response ($\overset{*}{E}IE$), which consisted of a discharge at the proximal surround, a suppression as the dark bar crossed the on-centre, followed by a stronger discharge as the bar entered the distal surround. In some cases a further weak suppression occurred as the bar left the distal off-surround ($E\overset{*}{I}EI$).

4.1.2. Off-centre cells:

Again, three types of centre-suppressed response patterns were found when tested with moving narrow light bars.

(i) $\overset{*}{E}IEI$-type: these cells exhibited a response pattern which consisted of a weak discharge as the bar crossed the proximal on-surround, a complete suppression of firing as the bar covered the off-centre, a vigorous discharge as the bar entered the distal on-surround and, finally, a weak suppression as the bar left the distal surround.

(ii) $\overset{*}{E}IE$-type: This comprised of vigorous discharges as the light bar entered both the proximal and distal surround regions, with a suppression of firing as the bar covered the off-centre.

(iii) $\overset{*}{I}EI$-type: No discharge was evoked as the bar crossed the proximal surround, with suppression as the bar crossed the centre, followed by a vigorous discharge and a final weak suppression as the bar entered and left the distal on-surround.

When tested with dark bars, an $\overset{*}{I}EI$-type of response pattern resulted, with suppressive effects as the bar crossed the proximal and distal on-surrounds and a strong discharge as the bar entered the off-

centre. For some cells, additional discharges occurred prior to the bar entering the proximal on-surround and/or on leaving the distal surround ($EIE\overset{*}{I}$ and $EIE\overset{*}{I}E$ or $IE\overset{*}{I}E$).

Both on-centre and off-centre cells were tested for the presence of directional selectivity in their response to oriented bars whose direction of motion was varied in 22.5° or 45° steps and no directional selectivity was observed (Fig. 23). However, in some cells the magnitude of the discharge peaks in the response patterns were different for directions of motion 180° apart. This differential response may reflect asymmetries in the strength of the component zones of the receptive fields (see later).

4.1.3. Sustained/Transient cell types:

The previous description of response patterns to moving bars indicates a range of complexity of response patterns.

The majority of 'brisk' sustained cells (70%) appeared to have the more complex response patterns containing additional discharge peaks and suppressions; while 'brisk' transient cells tended to possess the simpler types of response patterns e.g. $\overset{*}{E}I$ and $\overset{*}{E}IE$. However, following a detailed study of 'brisk' types (138 cells - see later) a correlation between 'brisk' sustained and 'brisk' transient cells with complex and simple patterns was less apparent. It was found that response patterns were not a stable characteristic of many cells (60%) for many components in the response pattern (i.e. the discharge peaks and suppressions) were dependent on a number of stimulus parameters, e.g. bar dimensions and velocity of motion - see later. The majority of 'sluggish' sustained and transient cell types

showed the simpler type of response pattern.

The nature of the response patterns was investigated in detail for 71 'brisk' sustained, 67 'brisk' transient, 21 'sluggish' sustained and 16 'sluggish' transient cells, and each of these cells was subsequently tested with textured 'visual noise' - see section 4.2.

Receptive field organization:

Receptive field centres were plotted as contours of iso-sensitivity to small light spots presented for 500 msec/sec, as described in Chapter 3.

Receptive field surrounds could be easily mapped for most 'brisk' sustained and 'brisk' transient cells with an exploratory flashing light spot of an appropriate size (i.e. 0.5°-1.5° or 1.0°-2.0° for 'brisk' sustained and 'brisk' transient cells respectively). In sluggish cells, surrounds were often more difficult to detect with an exploratory spot. Surround responses to spot presentations were always weaker than centre-evoked responses. An exploratory spot gave some clue to the potency of the receptive field surround, revealing a diminishing surround potency through 'brisk' sustained and 'brisk' transient down to the 'sluggish' types.

Cells for which surround responses to spot stimulation were weak or absent were subjected to one or more of the following tests in order to demonstrate an antagonistic surround, (in each case comparing gated spike counts during and following the stimulus):

(a) a series of concentrically presented annuli of varying diameter.

(b) adaptation of the receptive field centre with a light spot while exploring the surround with a second light spot or concentrically presented annuli (centre adaptation lowers its sensitivity while simultaneously raising that of the surround - Barlow et al, 1964; Wiesel & Hubel, 1966; Enroth-Cugell & Lennie, 1975).

(c) a series of concentric spots of varying diameter.

The result of spots covering part or all of the surround, in addition to the centre, was a surround discharge with a partial or total suppression of the centre response in 'brisk' sustained cells, for both 'brisk' transient and 'sluggish' cells large spot stimuli yielded net centre responses and only rarely were surround responses obtained. For three 'sluggish' transient cells, no surround could be revealed by any of these tests.

Most cells tended to have their strongest centre response near the geometric centre of the receptive field. However, for many cells it was situated asymmetrically. Similarly, for the surround region both symmetric and asymmetric organizations were found when mapping with an exploratory spot, either with or without centre adaptation. This asymmetry in the centre-surround organization was occasionally reflected in the firing patterns to moving bars in yielding differential responses to movement along different diameters as judged by the heights of the response peaks in PSTH's.

The presence of an additional outer annular zone synergistic with the centre has been described by Hammond (1972a,b; 1973) and Maffei & Fiorentini (1972) for lateral geniculate neurones. This outer disinhibitory surround will be discussed later (section 4.1.6.).

4.1.4. Response patterns - variation of bar dimensions:

Bar width: As reported by other authors, increasing bar width beyond the optimum results in an accentuation of the centre response, whether centre-activated or centre-suprressed. For centre-activated cells the response patterns are similar to those elicited by narrow bars, with the addition of an extended centre activation and a secondary peak in the centre response as the trailing edge of the bar enters the distal surround. In centre-suppressed cells, three response peaks are often present: a discharge as the leading edge enters the proximal surround; a suppression as the bar crosses the centre; a second discharge from the leading edge over the distal surround; a further suppression from the 'body' of the bar over the centre; a third discharge as the trailing edge crosses the centre; and finally suppression from the trailing edge crossing the distal surround.

Slow motion of an end-on bar through the receptive field, whose width approximates the receptive field diameter and of contrast appropriate to the receptive field centre, yields two types of response which may be correlated with sustained and transient cells. In sustained cells there is a plateau of elevated maintained firing, above that of the spontaneous firing rate, between two discharges elicited by the leading and trailing edges entering the receptive field centre, whereas, for transient cells, the 'plateau' falls to the spontaneous firing level. This distinction is readily demonstrable with long end-on bars (7-15°) at slow velocities 1-5°. sec^{-1}).

Bar length: Short, narrow bars of contrast appropriate to the receptive field centre yielded a response component dominated by the receptive field centre. Elongation of the bar resulted, for

increases in bar length of up to twice the centre diameter, in an increased centre response (for stimulus sizes up to approximately the centre diameter) and an enhanced surround response component. Further elongation resulted in a diminution of both centre and surround components, presumably as progressively more of the antagonistic surround was covered by the bar, so suppressing the centre component. If the bar extended beyond the surround, i.e. more than some four times the centre diameter, then the surround response component was also reduced. These observations are presented in Fig. 16 (a-c) and have been ascribed to the 'silent suppressive field' component by Levick et al (1972) and Dreher and Sanderson (1973). They will be further discussed with the outer (disinhibitory) surround later.

4.1.5. Response patterns - bar velocity:

As described in Chapter 3, 'brisk'/'sluggish', sustained and transient cells exhibited different velocity preferences. In addition to these, there are also characteristic velocity-related changes in both centre-activated and centre-suppressed response patterns.

For some centre-activated types there was little response from the surround component to slow moving bars (1.5°. sec^{-1}). However, the surround response increased in vigour at higher velocities (20-70°. sec^{-1}) - see Fig. 16. Conversely, for centre-suppressed types at slow velocities there was generally a suppression of firing as the bar left the distal surround, which was often absent at higher velocities (greater than 30°. sec^{-1}).

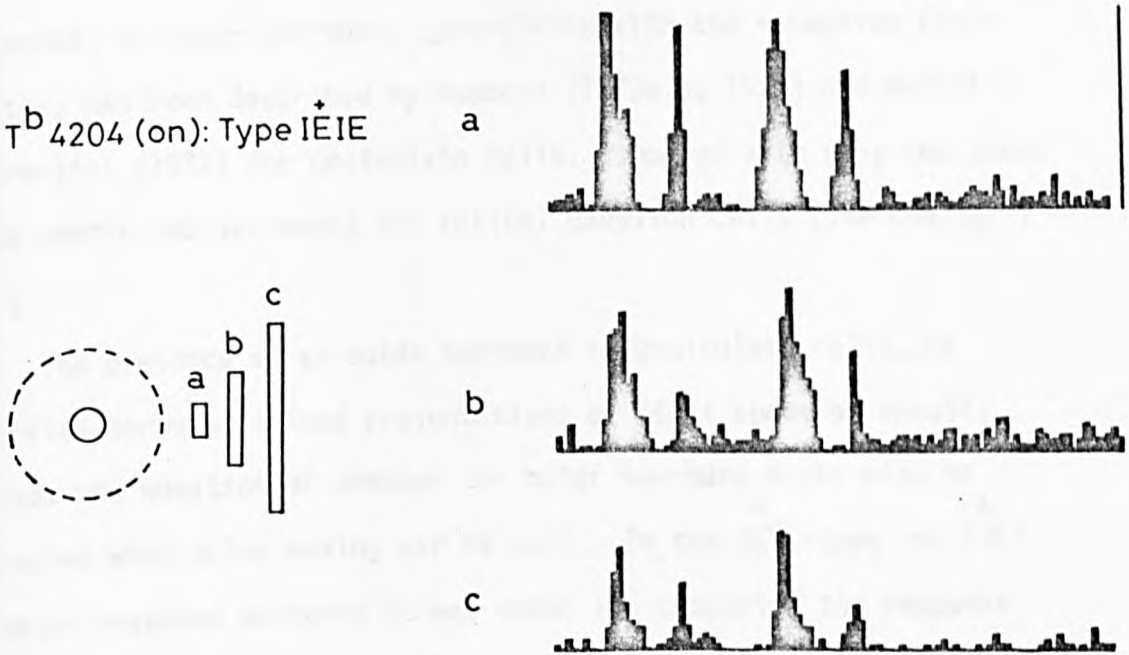
This velocity-related behaviour appeared to be independent of the sustained/transient classification, although the responses tended to be weaker in 'brisk' transient and 'sluggish' cell types, probably

Fig. 16.

(a-c): Response patterns from an on-centre cell to increasing length of moving light bars centred over the receptive field centre (a: 1 x 0.5°; b: 3 x 0.5°; c: 5 x 0.5°) at $10°.sec^{-1}$.

(d): Response of same cell to 1 x 0.5° bar moved at $4°.sec^{-1}$. Vertical bar calibration 50 impulses/bin; bin width 10.24 msec; sweep period 1 sec; PSTH's accumulated for 16 sweeps.

p


T^b 4204 (on): Type IÉIE
a
b
c
a
b
c

reflecting their weaker surround regions.

4.1.6. The outer surround:

In addition to the receptive field centre and antagonistic surround, an outer surround, synergistic with the receptive field centre, has been described by Hammond (1972a,b; 1973) and Maffei & Fiorentini (1972) for geniculate cells, compared with only two zones (the centre and surround) for retinal ganglion cells (see chapter 1 - 1.).

The presence of an outer surround in geniculate cells, as revealed through flashed presentations of light spots or annuli, raises the question of whether the outer surround might also be revealed when using moving bar stimuli. In the IEIE-type and EIEI-type of response patterns it was noted (in comparing the response pattern with the mapped receptive fields and by motion of bar stimuli through small excursions (less than 0.5°)), that movement of a narrow light bar, evoked a weak discharge from on-centre cells and a weak suppression from off-centre cells, as the bar left the distal surround. Such responses could derive from a luminance change as the bar left the distal surround and/or be due to stimulation of the outer surround zone.

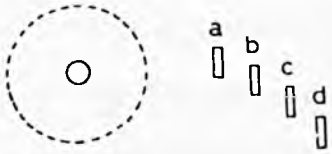
Ten cells were studied in detail for periods of 6-12 hours in order to undertake an 'activity profile' analysis of geniculate receptive fields after that of Bishop and co-workers for striate simple cells (Bishop et al, 1973). This comprised a series of 6-10 activity profiles (PSTH's) to short narrow (1°x0.5°) bars, of contrast appropriate to the receptive field centre, moved across the receptive field at various positions; between each PSTH, the bar was

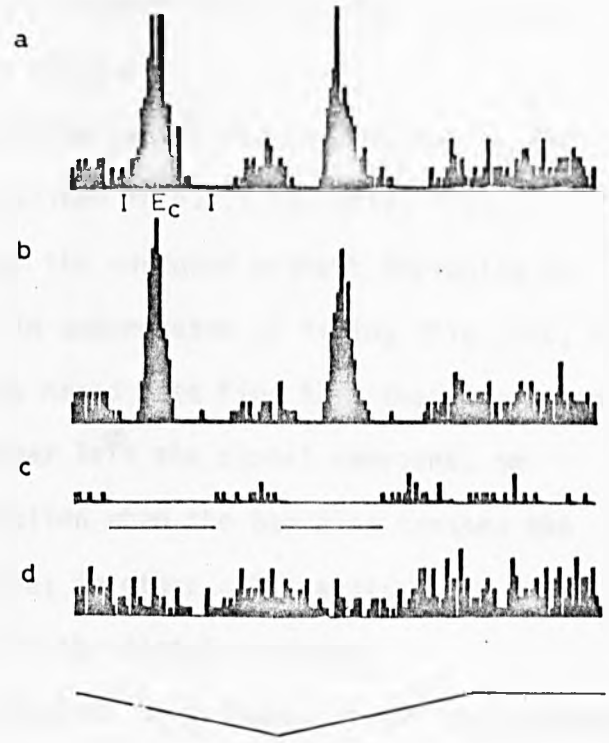
Fig. 17.

(a-g): Response patterns to a bar (1 x 0.5°) moved across the receptive field at various positions for an on- and off-centre 'brisk' sustained cells at 10°sec.$^{-1}$; one cell shows a complex response pattern (4509), the other a simple one (4507).

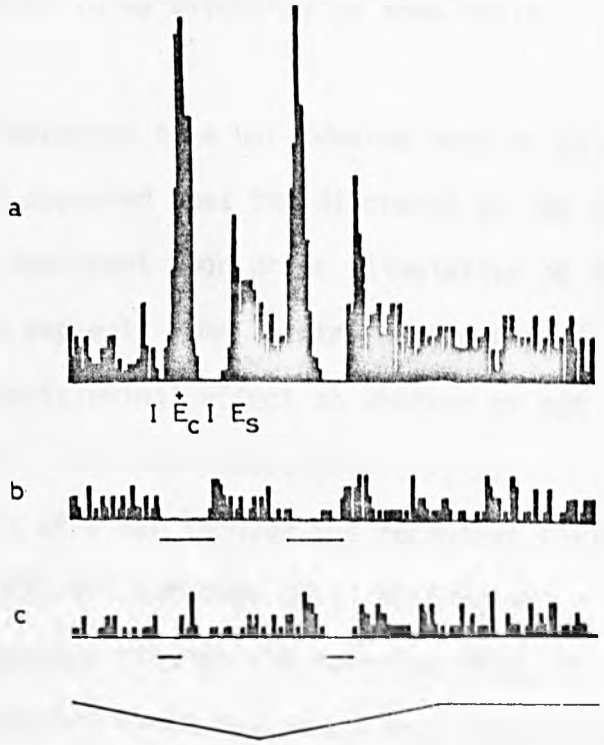
Details in Fig. 16.

S^b4507 (on): Type I$\dot{E}$I





S^b4509 (off): Type I$\dot{E}$IE



re-positioned by between half and one complete bar length. These results were as expected for a concentrically organized receptive field and may be summarized as follows:

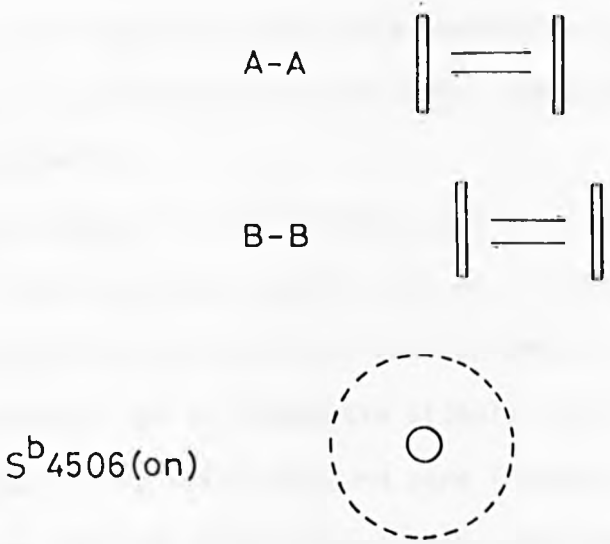
(i) a bar passing through the centre resulted in one of the response patterns outlined in 4.1.1./2. (Fig. 17e).

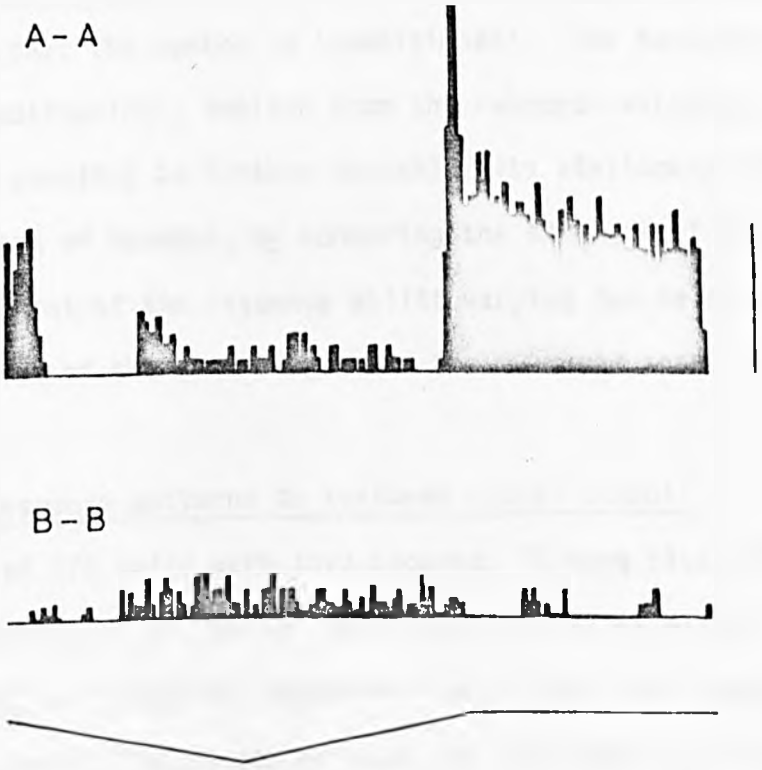
(ii) a bar passing through the surround without impinging on the centre resulted in suppression of firing (Fig. 17c, f). For some cells it was noted (see Fig. 17f) that there was no discharge as the bar left the distal surround, in contrast to the situation when the bar also crossed the receptive field centre; in other cells a discharge was elicited as a bar left the distal surround.

(iii) a bar which passed through the surround and/or the presumed outer surround zone (as assessed by flashed spot or annular stimuli) also resulted in no discharge in some cells (Fig. 17g).

For those cells which discharged as a bar crossed part or all of the receptive field centre it appeared that the discharge as the bar left the distal surround was dependent upon prior stimulation of the receptive field centre. This suggests some 'centre dependency' in which the centre has some 'conditioning' effect on whether or not there is a surround discharge. This was tested (Fig. 17) by accumulating PSTH's for motion of a bar through the receptive field which either included the centre and surround (Fig. 18 A-A) or which was offset so as to pass only through the surround (Fig. 18 B-B). Again, only in the situation where the centre was included in the stimulation was there a surround discharge present. This observation, coupled with the response-velocity functions regarding

FIG. 18. PSTH's for an on-centre 'brisk' sustained cell, recorded from layer A_1, accumulated for 16 sweeps of a moving light bar (2 x 0.5°) at a velocity of $10°.sec^{-1}$ for motion of the bar through the receptive field to include both the centre and surround (A-A) or only the surround (B-B). Bin width 10.24 msec.; sweep duration 2 secs; calibration 25 impulses/bin.


A-A
B-B
S^b4506(on)


A – A
B – B

the appearance of a strong surround discharge (4.1.5), suggest that temporal factors are important in mediating the surround discharge response which could be selectively enhanced at certain velocities; conversely, for centre-suppressed cells, the centre suppression was velocity dependent.

The discharge (or suppression) as a bar leaves the distal receptive field surround could be due to a 'disinhibitory' mechanism, activation of the outer surround zone or both. It could be argued that a moving bar is an inadequate stimulus for the known annular organization of the outer surround zone (Hammond, 1973). However, this annular zone was most obvious when annuli were flash-presented synchronously with spot over the receptive field centre - a conditioning stimulus (Hammond, 1973) and, as such, bears a resemblance to that of bar motion in that the centre is 'conditioned'. The temporal factor of centre 'conditioning', implied from the response-velocity functions may possibly be further testable with stationary stimuli, after the method of Hammond, by comparing the strength of the outer surround component of the response whilst varying the delay between the presentation of the centre spot and the surround annuli.

4.2. Response patterns to textured visual stimuli

A total of 175 cells were investigated; 71 were classified as 'brisk' sustained, 67 as 'brisk' transient, and 37 as either 'sluggish' sustained (21) or 'sluggish' transient (16). This cell sample constituted part of 'LGNd complex study II' (Chapter 3). Cells had receptive field centre sizes ranging between 0.5-1.25° for 'brisk' sustained, 0.75-3.5° for 'brisk' transient, and 2-4° for 'sluggish' cells. Retinal eccentricities ranged up to 30° and were confined

largely to the lower quandrant of the contralateral visual field.

Responses to motion of light, dark or static-noise bars against a stationary, randomly textured background of static noise were compared from dot displays and PSTH's for a range of velocities ($1\text{-}120°.sec^{-1}$) and average grain size of texture 3-20 min. of arc). Responses to motion of the textured background itself were compared over the same ranges. Each cell's maintained firing rate was assessed in the presence of the stationary background of visual noise.

4.2.1. On/Off centre cell responses:

Both on-centre and off-centre cells responded to motion of a bar of static noise against a similarly textured background. The responses resembled those elicited by a moving light or dark bar of contrast appropriate to the receptive field centre (81% of cells), i.e. a light bar in on-centre cells and a dark bar in off-centre cells (Fig. 19), or to the receptive field surround (19% of cells), despite the fact that there was no average luminance difference between the noise bar and its background.

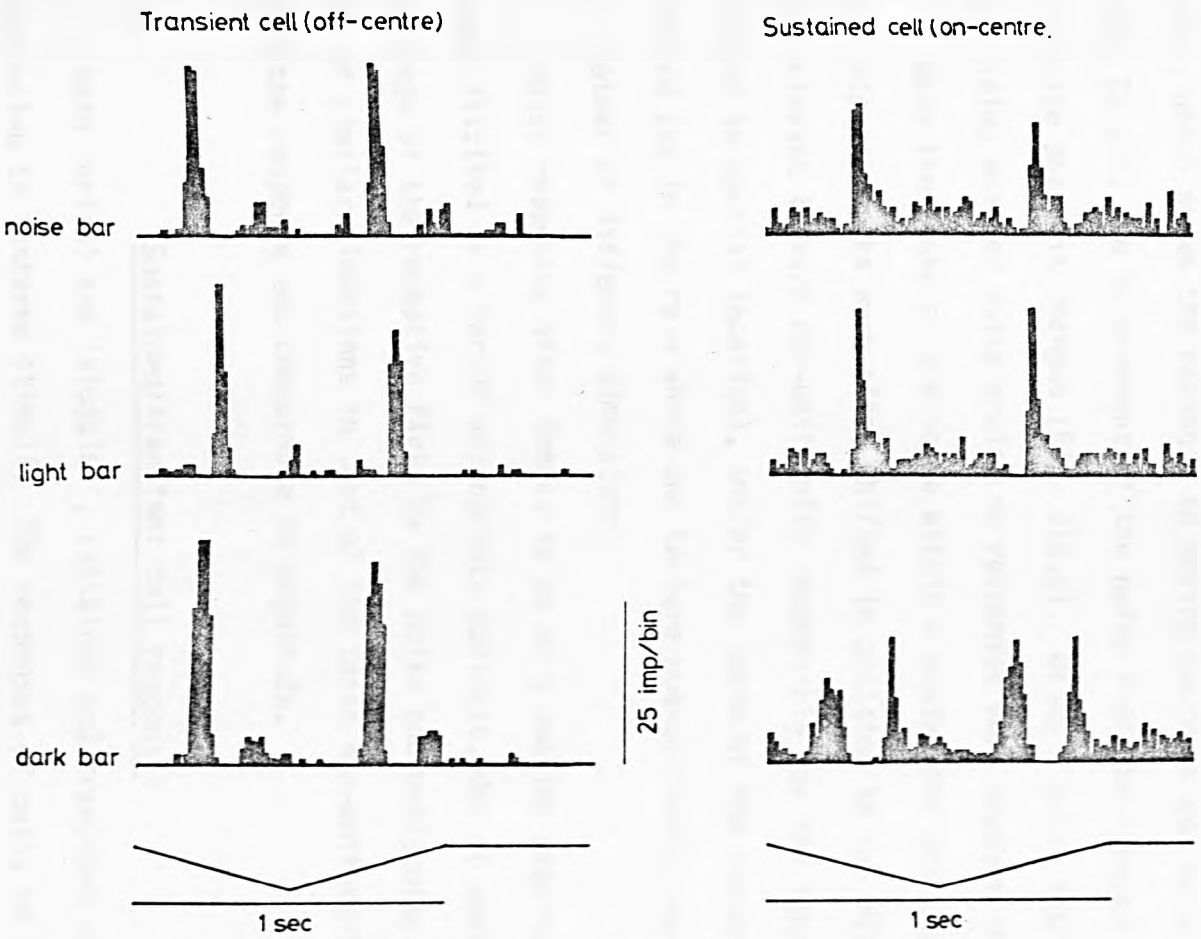
4.2.2. Phase and average grain size:

Systematic variation of the 'phase' and average grain size of the noise revealed that, e.g. for those cells with smallest receptive field centres (0.5°-1.0°), above an average grain size of 4-5 minutes of arc the random distribution of grain in the noise inevitably results in non-uniformities of texture sufficient to elicit a response to motion (Fig. 20). The critical grain size required to elicit a response was determined by changing the phase of the noise in a bar

Fig. 19.

PSTH's for an off-centre 'brisk' transient and on-centre 'brisk' sustained cell, recorded from layer A, accumulated for 16 sweeps of moving light, dark and noise squares (1 x 1°) at a velocity of $10°.sec^{-1}$; bin width 10.24 msec.

Lower insert; a typical sample of static visual noise.


Transient cell (off-centre)
Sustained cell (on-centre.
noise bar
light bar
dark bar
25 imp/bin
1 sec
1 sec

approximately twice the receptive field centre diameter in width, positioned over the receptive field centre, for a range of average grain sizes (achieved through variation of the overall dimensions of the frame of the noise background). This is shown in Fig. 21 (a-f), which shows the response to moving contrast and noise bars (Fig. 22 a-c) and to movement of the noise field background in which the noise phase is changed (Fig. 21d,e). Using a noise field containing smaller noise grain, no responses were present (Fig. 21f).

When the phase of the noise within a moving bar was changed, the response peaks were often shifted in position in the PSTH (as the relevant texture non-uniformity responsible for the response shifted in spatial location), and/or the shape of the response peaks altered (as in the case where one texture non-uniformity was replaced by another of different dimensions).

Noise responses often tended to be of a smaller magnitude than those elicited by a bar of appropriate contrast, due to smaller coverage of the receptive field by the noise non-uniformity. If a bar of similar dimensions to that of the noise non-uniformity was used the response was comparable in magnitude.

4.3. Sustained/Transient cell response:

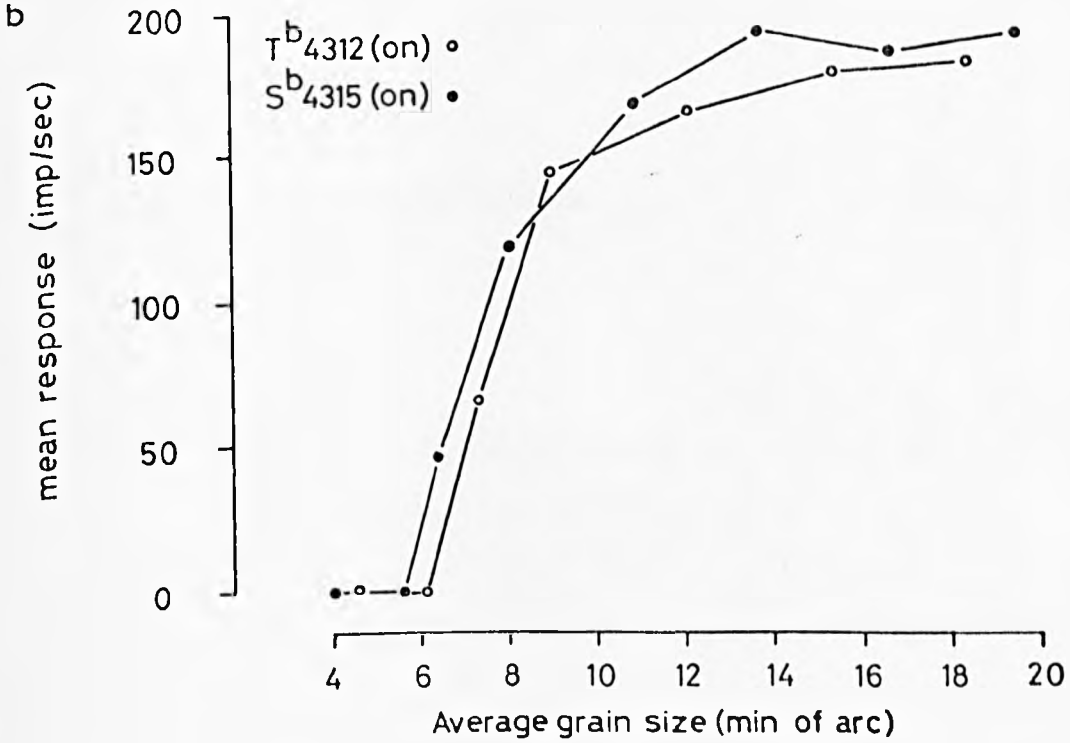
Both 'brisk' and 'sluggish', sustained and transient cells were responsive to textured stimuli. The responses of cells in the MIN matched those of cells recorded in the laminated LGNd.

'Brisk' transient and 'sluggish' cell types tended to require a larger average grain size than 'brisk' sustained cells to elicit a response, a tendency apparently related to the receptive field centre size (Fig. 20). Increasing the average grain size, with resultant

Fig. 20.

(a): A selected (random) sample of 'brisk' sustained (filled circles), 'brisk' transient (open circles) and 'sluggish' sustained and transient cells (filled and open triangles respectively), to show the minimal (threshold) average grain size capable of evoking a response to motion of a noise bar or noise field as a function of receptive field centre size.

(b): Examples of two on-centre, 'brisk' cells showing the change in response to increasing the average grain size of a moving noise field.


b
200
150
100
50
0
mean response (imp/sec)
T b 4312 (on)
S b 4315 (on)
4
6
8
10
12
14
16
18
20
Average grain size (min of arc)

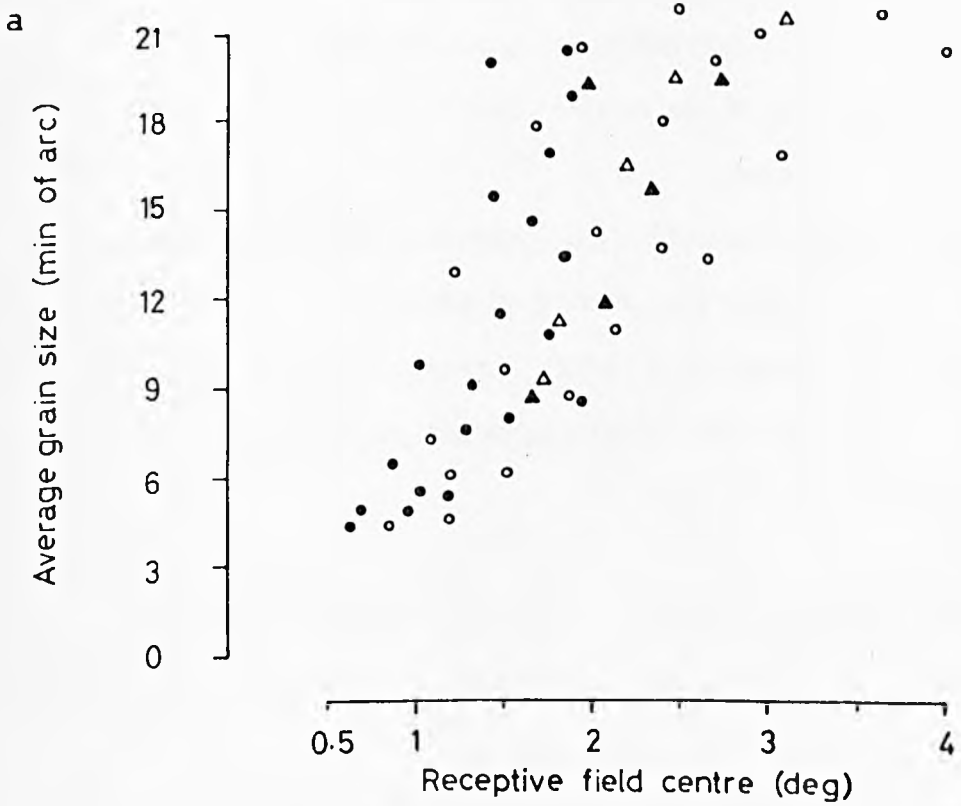

a
21
18
15
12
9
6
3
0
Average grain size (min of arc)
0·5
1
2
3
4
Receptive field centre (deg)

Fig. 21.

(a-c): PSTH's to moving dark, light and noise squares; details as in Fig. 17.

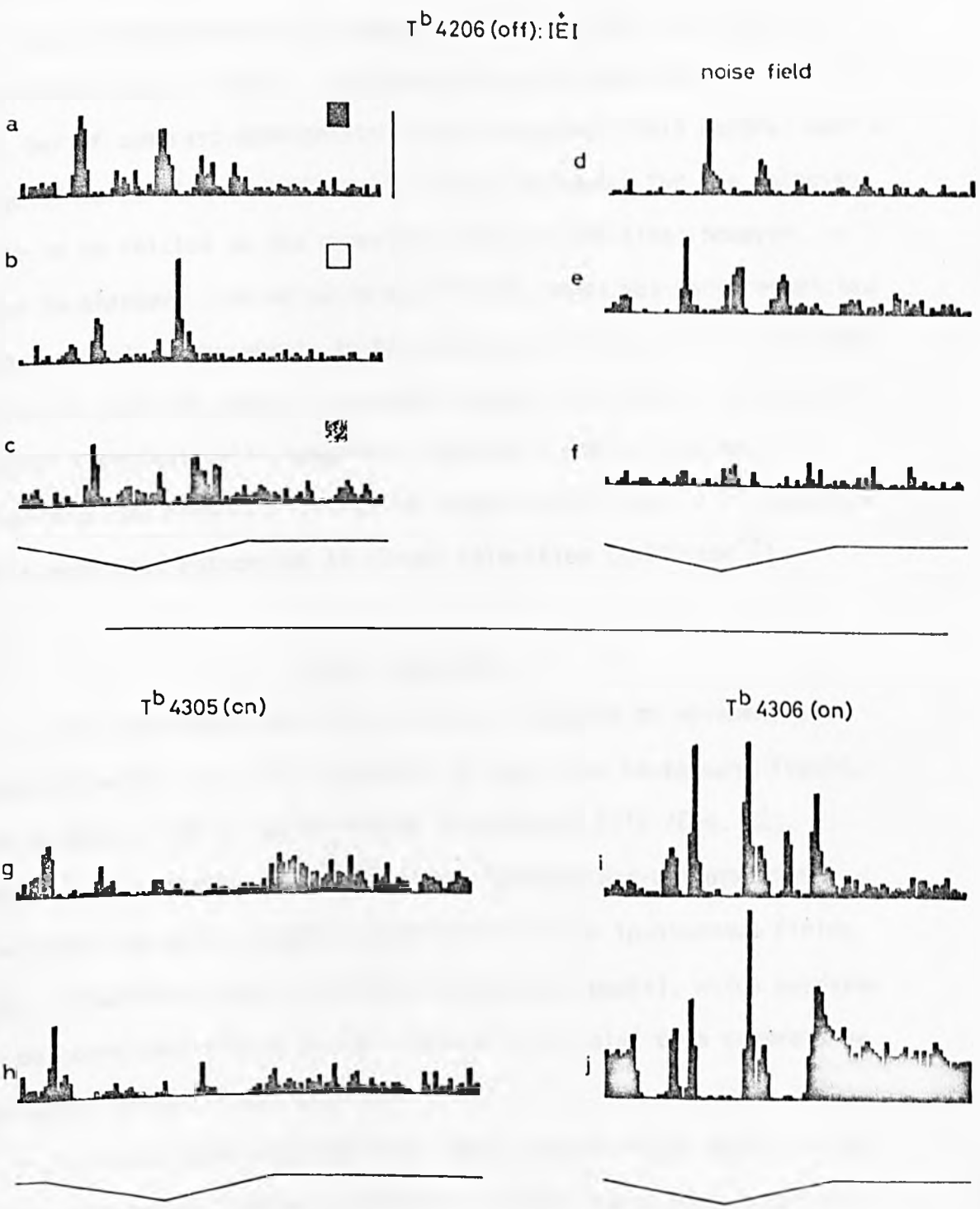
(d-e): PSTH's for motion of a static-noise field (average grain size 8 min of arc) before and after a change in phase of the noise.

(f) : PSTH for motion of a static noise field with smaller average grain size (5 min of arc).

(g-h): Response of a 'brisk' transient cell with a strong periphery effect/'silent suppressive surround' to noise field motion.

(i-j): Polymodal PSTH response pattern to noise field motion more commonly found. In (j) an EEG change occurred, associated with an elevated maintained firing rate and the disappearance of one response peak.

PSTH's accumulated over 16 sweeps; sweep duration 2 sec; bin width 10.24 msec.


T^b 4206 (off): IĖI
noise field
a
b
c
d
e
f
T^b 4305 (on)
T^b 4306 (on)
g
h
i
j

larger texture non-uniformities, led to increased response magnitudes. Similar increases in response magnitude obtained with moving spots or bars when their dimensions were increased.

Cells exhibited similar response-velocity functions with noise or contrast bars. 'Brisk' sustained cells responded well, to motion of a bar of contrast appropriate to the receptive field centre, over a range of velocities (1-100°.sec^{-1}), with a tendency for the velocity range to be related to the receptive field centre size; however, as noted in chapter the velocity sensitivity range was more restricted when a stimulus appropriate to the receptive field surround was used. Cells with smaller centres preferred slower velocities. In contrast, 'brisk' transient cells responded relatively poorly at slower velocities but vigorously at faster ones (30-120°.sec^{-1}). 'Sluggish' cells were most responsive at slower velocities (1-30°.sec^{-1}).

4.4. Other properties

Cells exhibited one of two types of response to movement of a broad noise bar (e.g. 10° in width) or the noise background itself. Approximately 80% of cells yielded a polymodal PSTH (Fig. 22), a result of responding to a multiple of 'texture non-uniformities'. The remaining cells showed a suppression of the spontaneous firing rate (occasionally with superimposed response peaks), which appeared to be correlated with a strong 'suppressive field' or a suppressive periphery effect (Fig. 21g,h).

It was further observed that, when using an oscillating noise field (the noise field was restricted using a card, with a circle 2-4° diameter cut-out, positioned over the cell's receptive field as a precaution against activation of the 'silent suppressive surround'

or periphery effect) containing smaller noise grain sizes where only a few or even no noise non-uniformities were present, many cells (8/15) exhibited an elevated mean discharge, which was reduced in magnitude when progressively smaller noise grain sizes were used; other cells (7/15) did not show this elevated mean discharge. These observations are presented in Fig. 22 from which it can be seen that those cells which exhibit this elevated mean discharge show a flatter response curve near threshold grain size than do the other cells (Fig. 21b). Both on- and off-centre, and 'brisk' sustained and transient cells were found to show either of these properties (no sluggish cells were subject to this test). Although based on a small cell sample, most such cells were 'brisk' transient (6/9). This property bears some similarity to the behaviour of X and Y retinal ganglion cells reported by Enroth-Cugell and Robson (1966) with respect to drifting gratings; however, as no square or sinusoidal grating facilities were available for the CRT display, the crucial tests for linearity could not be carried out. As discussed in chapter 1, the X/Y classification of Enroth-Cugell and Robson, based on spatial summation properties, is not necessarily equivalent to the sustained/transient classification, at least at the geniculate level (Shapley & Hochstein, 1975). Thus, if these observations are associated with the X/Y spatial summation properties, they could explain why both sustained and transient cells in the present study showed an elevated mean discharge for noise field movement.

As noted earlier, no 'brisk'/'sluggish' sustained or transient cells were directionally selective to stimulus motion along different axes, with the exception of occasional quantitative differences in response peaks, as described in section 4.1.3. A similar situation

Fig. 22.

Response patterns to motion of a noise field restricted to the central 2-3° of the receptive field (using a masking card), at an average grain size of 7 min. of arc. Some cells responded with an elevated discharge during movement (b); while for others no response was apparent, or a slight suppression was apparent (a).

Variation in the mean response to changing the average grain size is shown graphically to the right of the PSTH's.

PSTH's accumulated over 16 sweeps; vertical bar calibration 15 impulses/bin; bin width 10.24 msec; dotted line indicates the maintained firing rate to a stationary noise field.

a

T^b_{4209}

b

T^b_{4211}

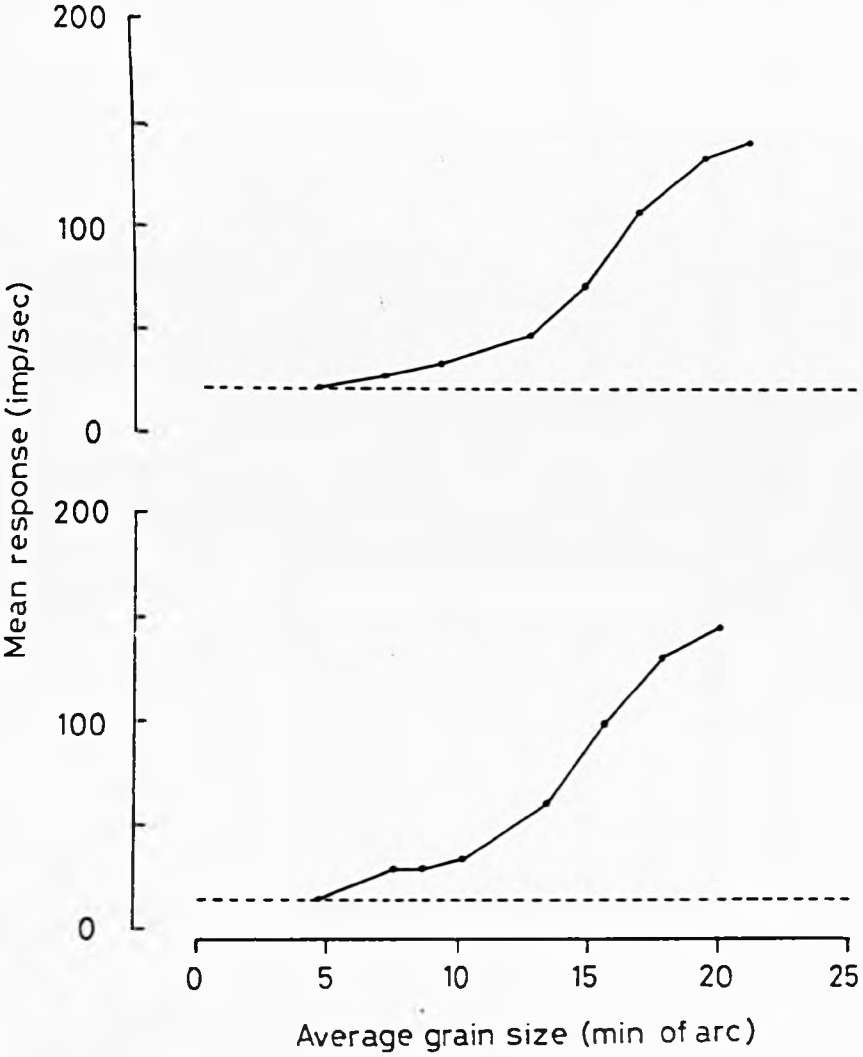
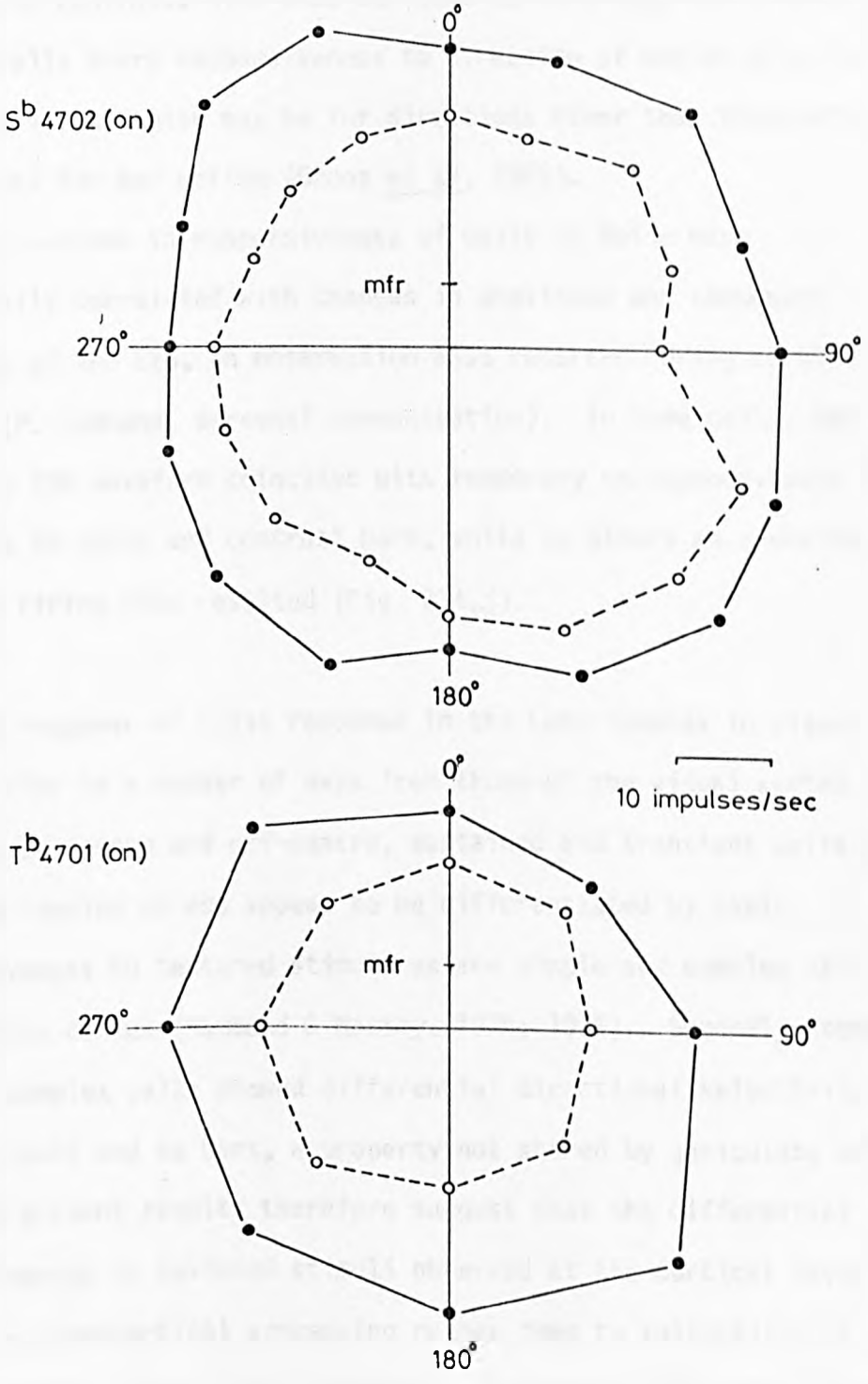

200
100
0
200
100
0
Mean response (imp/sec)
0
5
10
15
20
25
Average grain size (min of arc)

Fig. 23.

Polar plot of the direction sensitivity of a 'brisk' sustained and a 'brisk' transient cell to motion of a light bar (filled symbols) and a bar of static visual noise (open symbols).

Bar size 2 x 0.5°; velocity 15°.sec^{-1}; mfr - maintained firing rate.


0°
S^b 4702 (on)
mfr
270°
90°
180°
0°
10 impulses/sec
T^b 4701 (on)
mfr
270°
90°
180°

obtained for motion of a noise bar against a noise background, or for motion of the noise background itself (Fig. 23). This observation contrasts with that for some texture-responsive striate complex cells where responsiveness to direction of motion of a field of static visual noise may be for directions other than those which are optimal for bar motion (Groos et al, 1976).

Fluctuations in responsiveness of cells to noise were occasionally correlated with changes in amplitude and component frequency of the EEG, an observation also reported during cortical studies (P. Hammond, personal communication). In some cells, this change in EEG waveform coincided with temporary unresponsiveness of LGN cells to noise and contrast bars, while in others an elevation of the mean firing rate resulted (Fig. 21i,j).

The response of cells recorded in the LGNd complex to visual noise differ in a number of ways from those of the visual cortex. Firstly, on-centre and off-centre, sustained and transient cells in the LGNd complex do not appear to be differentiated by their responsiveness to textured stimuli as are simple and complex cells in the striate cortex (Hammond & MacKay, 1975; 1976). Secondly, some striate complex cells showed differential directional selectivity to noise stimuli and to bars, a property not shared by geniculate cells.

The present results therefore suggest that the differential responsiveness to textured stimuli observed at the cortical level must be due to intracortical processing rather than to selectivity at earlier stages in the visual pathway. In addition, the lack of any differentiation of cell types in the LGNd complex using textured visual noise provides no clue as to any differential function related to

visual texture which may have been correlated with neuronal organization within the constituent nuclei of the LGNd complex, for example 'brisk' transient cells whether recorded from the MIN or the laminated LGNd responded in a similar fashion.

Chapter 5

THE PULVINAR-COMPLEX: NEURONAL ORGANIZATION:

5.1. In addition to recording from the laminated LGNd and MIN, cells were often isolated from the adjacent nuclei of the lateral and posterior thalamic groups, in particular the pulvinar-complex. These observations were extended by investigating the response properties of cells recorded within the pulvinar-complex, using multiple penetrations in four cats under N_2O/O_2 supplemented with sodium pentobarbitone.

Although the stereotaxic atlases of Jasper and Ajmone-Marsan (1954) and Snider & Niemer (1963), together with observations during individual experiments, were used for appropriate electrode placements the thalamic nuclei were classified according to Niimi and Kuwahara's (1973) cytoarchitectural study (as outlined in 1.3.) summarized as follows:

inferior pulvinar	=	posterior nucleus (PN)
lateral pulvinar	=	pulvinar nucleus (Pul)
medial pulvinar	=	major portion of the lateral posterior nucleus (LPN)
suprageniculate nucleus	=	suprageniculate nucleus (SG)
posterior lateral nucleus	=	anterior portion of the LPN

5.2. Receptive field properties:

A total of 192 cells were recorded from the extrageniculate visual nuclei in 32 cats (all but four cats were also used for geniculate recording). All cells exhibited some degree of spontaneous activity, with maintained firing rates ranging between

1-10 spikes.sec^{-1} to 5 spikes.min^{-1} for the majority of cells. A few cells showed a bursting type of maintained discharge consisting of spike clusters of 3-10 spikes every 20-60 secs. About 60% (117) of cells could be driven by visual stimuli and, together with non-visually responsive cells, were found distributed throughout the nuclei of the lateral and posterior thalamic groups. In addition to isolated unit recordings, records of multiunit activity also proved valuable when mapping the visual field.

Four electrode approaches were attempted. These included serial vertical and oblique (latero-medial) penetrations made during investigations of the LGNd complex and two oblique approaches (in a medio-lateral or medio-lateral/rostro-caudal direction).

Characteristic of recordings from the LGNd complex is the presence of background visual 'swish' to flashed stimuli; however, as electrodes enter the inferior pulvinar this background swish becomes fainter and often absent. Accompanying this is a second reversal in the trend of receptive field azimuth as the inferior pulvinar/MIN border is traversed (the first reversal occurring at the laminated LGNd/MIN border - see chapter 3). Recordings from the pulvinar-complex were further distinguished from the LGNd complex by the difference of receptive field types.

5.2.1. Receptive field types:

Visually responsive cells were assessed using flashed and moving stimuli and most cells (109/117) had one of the following receptive field types (see Table 3 for distribution of cell types in the pulvinar-complex).

Table 3: Pulvinar-complex study

	Diffuse	Concentric	Movement	Direction	Orientation	Others	Non-responsive
Inferior pulvinar	4	4	5	29	2	1	14
Medial pulvinar	5	2	9	13	—	4	23
Lateral pulvinar	3	2	7	6	5	3	21
Suprageniculate n.	1	—	5	—	—	—	5
Posterior lateral n.	4	—	3	—	—	—	12
	17	8	29	48	7	8	75

Diffuse (17):

These cells yielded on, off or on-off responses only to large spots or to diffuse flashes of light; moving stimuli were ineffective in eliciting responses. For most of these cells (12) it was not possible to determine any receptive field boundaries. The remaining seven cells had receptive fields some 10-90° in diameter with demonstrable receptive field boundaries; stimulation directed outside the boundary did not appear to affect receptive field stimulation.

Concentric (8):

These cells possessed an ovoid concentric centre-surround organization resembling that of retinal ganglion and geniculate cells. Both on- or off-centre cells were found with centres 2-10° in diameter and having phasic responses to flashed spots. The receptive field surrounds were weakly antagonistic, when compared with sustained cells recorded from the LGNd complex. When cells were assessed with tests used to characterize 'brisk', 'sluggish', sustained and transient cells in the LGNd complex the responses resembled those of 'sluggish' transient cells.

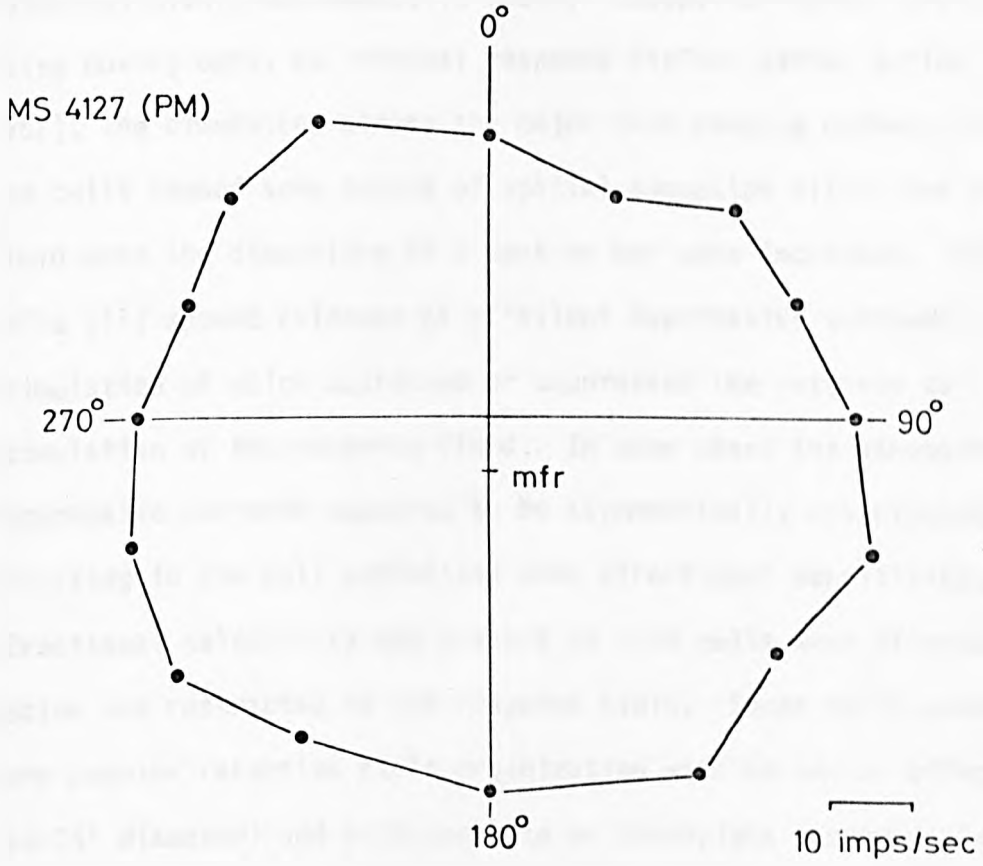
Movement sensitive (29):

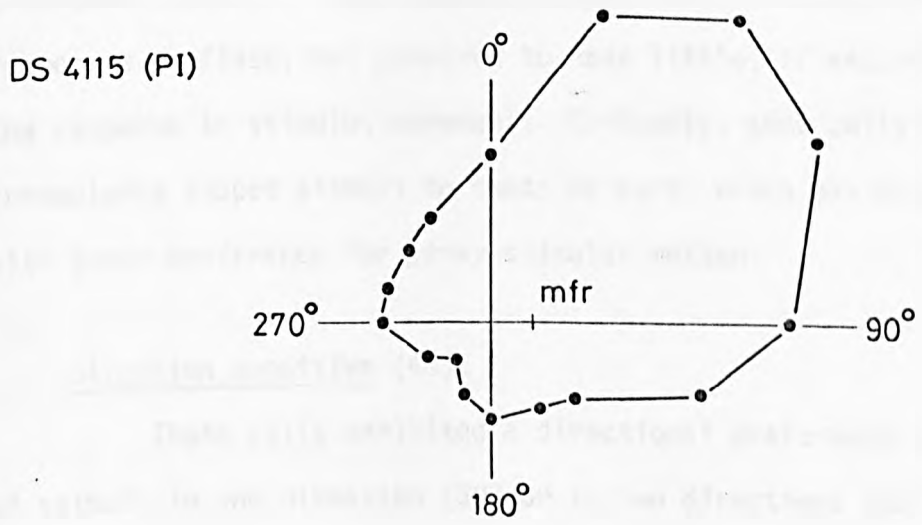
Such cells responded well to moving light and/or dark stimuli swept across the receptive field in any direction (Fig. 24), generally irrespective of stimulus shape. Most of the movement sensitive cells (as well as direction and orientation sensitive cells) responded over a broad range of stimulus velocities, ranging between 5-10°.sec^{-1} to over 120°.sec^{-1}; rarely responding at slow velocities (less than 5°.sec^{-1}). Many cells (15) appeared to respond better to jerky stimulus motions, (apparently corresponding to previous

Fig. 24.

Polar plot of the direction sensitivity of a movement sensitive cell (MS 4127), recorded from the inferior pulvinar, and a direction sensitive cell (DS 4115), recorded from the medial pulvinar to motion of a light bar.

Response mean of 16 sweeps; bar size 5 x 2°; velocity 20°.sec^{-1}; mfr - maintained firing rate.


MS 4127 (PM)
0°
270°
90°
mfr
180°
10 imps/sec


DS 4115 (PI)
0°
mfr
270°
90°
180°

descriptions of 'discontinuous movement' units recorded in the cat's medial and lateral pulvinar nuclei - Wright, 1971; Wright & Ikeda, 1973). Flashed stimuli elicited weak and often inconsistent on-off responses within the receptive field. Receptive fields were mapped, using moving bars, as 'minimal response fields' (after Barlow et al, 1967), the dimensions across the major axes ranging between 7-40°. Ten cells showed some degree of spatial summation within the response field when the dimensions of a spot or bar were increased. Other cells (11) showed evidence of a 'silent suppressive surround', stimulation of which depressed or suppressed the response to stimulation of the response field. In some cases the strength of this suppressive surround appeared to be asymmetrically distributed, often resulting in the cell exhibiting some directional sensitivity; no directional selectivity was present in such cells when stimulus motion was restricted to the response field. Seven cells possessed a more complex receptive field organization with an on- or off-centre (10-15° diameter) and with complete or incomplete surrounds (extending a further 20-30°). These surround zones were 'active', with on-off responses to flash, but appeared to have little, if any, effect on the response to stimulus movement. Curiously, some cells preferred irregularly shaped stimuli to spots or bars, which may be correlated with their preference for jerky stimulus motion.

Direction sensitive (48):

These cells exhibited a directional preference to movement of stimuli in one direction (30) or to two directions 180° apart (18). For some cells a suppression in the maintained discharge was clearly visible in the PSTH for the null direction of movement.

Although routine tests were not made, three cells (located in the lateral pulvinar) showed a preference for stimuli moving in the midsaggital plane towards (z+:2 cells) or away from z-:1 cell) the animal, with only a weak response to horizontal or vertical movements. However, movement of two edges towards or away from each other within the cell's receptive field effectively drove z- or z+ cells respectively. Interestingly, similar cells (opposed movement complex cells) have been described in the posterior bank of the superior temporal sulcus of rhesus monkey (Zeki, 1974c). Most cells were responsive over a wide range of directions of movement, responding well to motion up to 20-90° from the preferred direction. The distribution of preferred direction for the forty-eight direction sensitive cells is given in Fig. 25a. These results showed little, if any, directional trend for motion in the visual field; this contrasts with reports of a direction tendency towards the upper temporal portion of the visual field found in the cat's superior colliculus (Berman & Cynader, 1972) and the pulvinar-complex (Godfraind et al 1972). Reversing the stimulus contrast had no effect on the preferred directions exhibited by individual cells. In no case was there any evidence of a surround zone in direction sensitive cells such as found in some movement sensitive cells. Flashed light or dark stimuli were generally ineffective in eliciting responses. Responses fields were defined as 'minimal response fields' and ranged between 10-40° across.

Orientation sensitive (7):

These cells responded optimally to light or dark edges oriented perpendicular to the preferred direction of movement; light or dark spots elicited only weak responses. Orientation tuning for

these cells tended to be broad (cf cortical simple cells), and cells were still responsive to orientations up to 80° away from the optimum. Response field dimensions ranged between 8-25° across. There was no evidence of any suppressive surround region as judged by extending bar length beyond the response field borders. Again, responses to flashed stimuli were weak, inconsistent and often absent.

Other cells (8):

A problem which was encountered with almost all of the cells recorded in the pulvinar-complex was their adaptation to repeated visual stimulation. This property varied between cells and for some it was necessary to use long interstimulus intervals, often up to 2 mins, in order to obtain repeatable results. This problem was so accentuated for six cells that it was not possible to reliably assess the cell's response properties, although these cells were responsive, albeit intermittently, to visual stimuli.

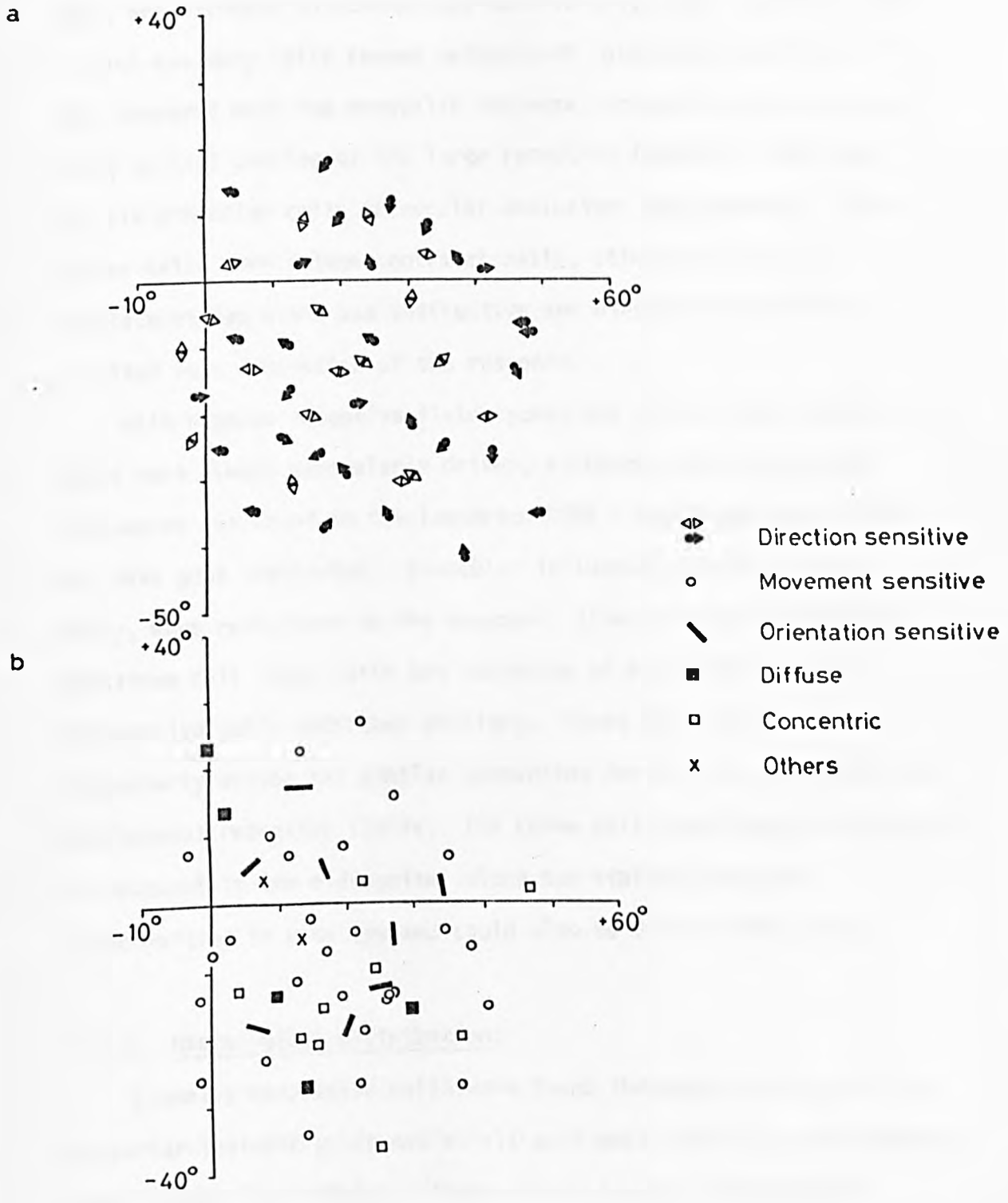
The remaining cells (2) are best described as 'binocular suppressive' in that their maintained firing rate was suppressed when stimuli (spots or bars) were moved through their receptive fields. Flashed stimuli were less effective in suppressing the maintained discharge. No excitatory responses could be demonstrated using either flashed or moving stimuli. This suppression could be elicited through either eye, or binocularly.

5.2.2. Ocular dominance:

Due to problems of adaptation to visual stimuli it was difficult to categorize ocular dominance reliably after the scheme of Hubel & Wiesel (1962). Overall, however, 53% (62) of cells were driven exclusively by the contralateral eye, 9% (11) of cells were driven

Fig. 25.

Distribution in the visual field of the receptive field centre points of cells recorded from the pulvinar-complex. In (a) the double arrow heads represent bidirection sensitive cells.


a
+40°
-10°
+60°
-50°
b
+40°
-10°
+60°
-40°
Direction sensitive
Movement sensitive
Orientation sensitive
Diffuse
Concentric
Others

ipsilaterally and the remaining 38% (44) were binocularly influenced. The majority of binocular cells (38) were actively driven by both eyes, and although no attempt was made to align the receptive fields of each eye many cells showed evidence of 'bincoular facilitation' when compared with the monocular response, probably accounted by at least partial overlap of the large receptive fields for each eye. For six binocular cells 'binocular occlusion' was apparent. These latter cells were driven contralaterally; stimulation of the ipsilateral eye alone was ineffective and binocular stimulation resulted in a diminution of the response.

With regards receptive field types, the diffuse and concentric types were always monocularly driven, although subtle binocular influences (as found in the laminated LGNd - Sanderson et al, 1971) may have gone undetected. Binocular influences, in the present study, were restricted to the movement, direction and orientation sensitive cell types (with the exception of two binocularly suppressive cells described earlier). Those cells which could be binocularly driven had similar properties for both contralateral and ipsilateral receptive fields. The three cells sensitive to direction of movement in the midsaggital plane had similar direction selectivities in each eye and could also be driven monocularly.

5.2.3. Histological distribution:

Visually responsive cells were found throughout the lateral and posterior thalamic group nuclei although most (104/117) were recorded from the pulvinar-complex. There was no apparent differential distribution of receptive field types which could be correlated with nuclear cytoarchitecture (see Table 3), with the exception of a

preponderance of direction sensitive cells (65%) in the inferior pulvinar. However only diffuse (1 and 4 cells) and movement sensitive (3 and 5 cells) receptive field types were recorded from the supragenículate and posterior lateral nuclei respectively, a bias probably reflecting the small cell sample of these nuclei (13 visual and 17 non-responsive cells). Similarly, non-responsive cells were found distributed throughout the lateral and posterior thalamic groups and were intermingled with visually response cells. However, the proportion of non-responsive to visually responsive cells recorded varied between animals. In some cats it was comparatively easy to drive cells visually, while in others cells were more difficult to drive. These factors probably reflect a deterioration of the preparation (there was a tendency for this to occur during the second day of a preparation, which was one of the reasons that four cats were used solely for pulvinar-complex recording) and/or variation between cats in their susceptibility to anaesthesia. It is probable that many visually responsive cells were missed through using inadequate stimuli, a universal problem encountered in sensory physiology.

5.3. Visuotopic organization:

Inferior pulvinar:

Observations regarding visuotopic organization within the inferior pulvinar are essentially similar to those reported by Kinston et al (1969). Recordings from the inferior pulvinar were frequently obtained, at various anterior-posterior placements, during serial vertical and oblique electrode approaches made during investigations

of the LGNd complex and a second reversal in the trend of receptive field azimuth was observed as the MIN/inferior pulvinar border was traversed. The arrangement of azimuth across the inferior pulvinar resembles that found in the laminated LGNd, with central azimuth values represented medially and peripheral azimuth values laterally. Azimuth ranged from about 50° peripherally in the contralateral visual hemifield, extending across the vertical meridian up to 10° in to the ipsilateral hemifield. The range of receptive field elevations contained within the inferior pulvinar appeared to be restricted largely to the lower visual hemifield, rarely extending more than 10° into the upper visual hemifield. The horizontal meridian was represented superiorly in the inferior pulvinar with successively lower elevations represented inferiorly. With the exception of a slight tendency for cells with receptive field elevations extending more than 5° into the upper visual field to be located more posteriorly within the inferior pulvinar there was little evidence of any anteroposterior organization of elevation values.

Medial pulvinar:

The visuotopic organization in the medial pulvinar appears more complex than that present in the inferior pulvinar. Cells with receptive fields in the upper visual field were found throughout most of the antero-posterior extent of the medial pulvinar. Rostrally such cells were located dorso-laterally while caudally their location was shifted more ventrally until lying adjacent to the caudal pole of the LGNd complex, a shift coincident with the diminishing nuclear boundary of the medial pulvinar at its posterior extent. From the present cell sample there appeared to be a more restricted

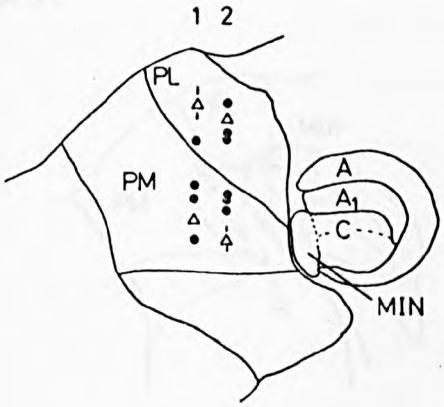
representation of the upper visual field, compared with the lower visual field, rarely extending more than 35° from the area centralis. The lower visual field was represented ventro-laterally and rostrally in the medial pulvinar, while caudally it appeared to merge imperceptibly with the representation of the lower visual field contained within the inferior pulvinar. There was no evidence of lower visual field representation at the most caudal pole of the pulvinar-complex where only the medial pulvinar is present. An organization of receptive field azimuth values in the medial pulvinar was also apparent which resembled that found within the inferior pulvinar and with which it appeared to be continuous. It was also observed that most of the cells in the visuotopically organized region were of the direction sensitive type which were commonly found in the inferior pulvinar. However, although a visuotopic progression was apparent, albeit a coarse representation, particularly dorso-laterally in the medial pulvinar the receptive fields of cells located more ventrally tended to be more randomly organized. As found for the more dorsally situated cells, there was nevertheless a tendency for the upper and lower visual field representations to be found dorsally and ventrally respectively. The representation of the visual field in the inferior and medial pulvinar nuclei is illustrated at four levels in the pulvinar-complex in Fig. 26.

Anatomical studies of tecto- and cortico-thalamic projections (Graybiel, 1972; Kawamura et al, 1974; Kawamura, 1974) have demonstrated a striate projection zone inclined rostro-caudally and medio-laterally lying dorsal and adjacent to a tectal projection zone. The possibility of a correlation between these anatomical zones and differences between dorsally and ventrally recorded cells prompted

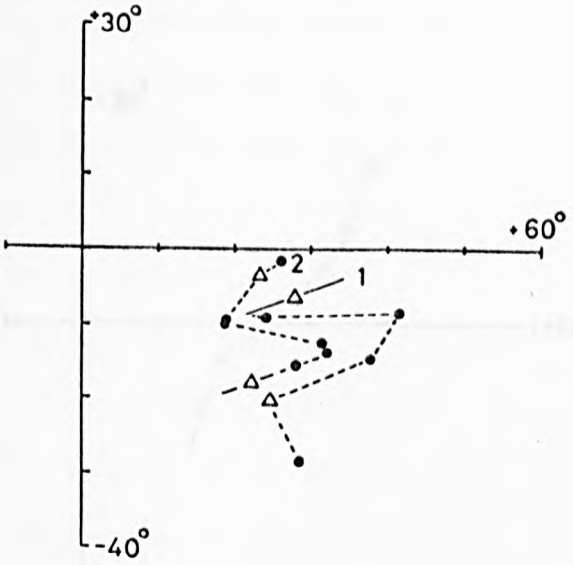
Fig. 26.

The locations in the pulvinar-complex of visually responsive single cells (filled circles) and multiunit activity (open triangles) and the positions of their receptive field centres in the visual field at four levels (Horseley-Clarke coordinates A 7.5, 6.5, 5.5, 4.5). The bars extending through the multiunit triangles represent the extent over which visually responsive activity was recorded.

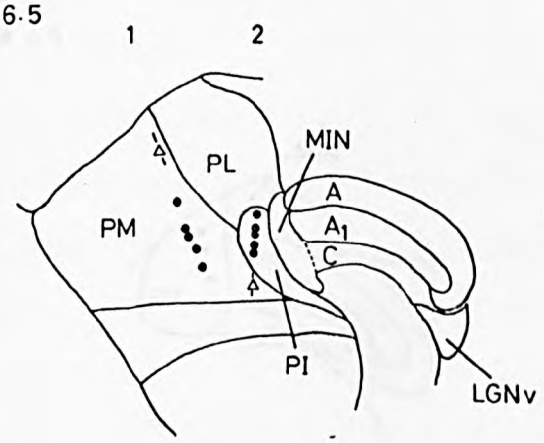
a) A 7·5

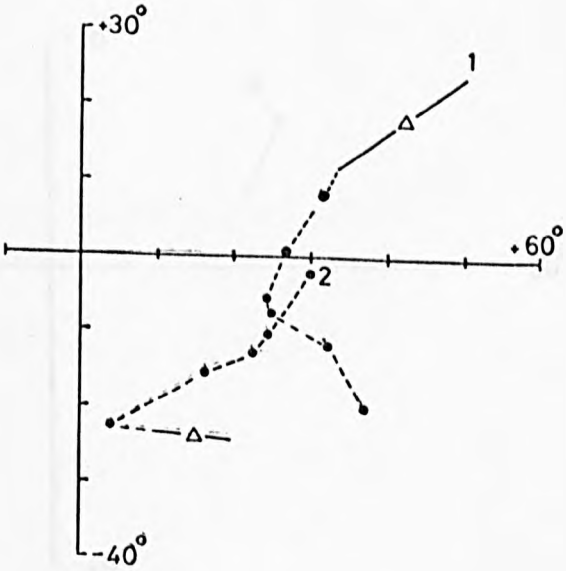


2mm

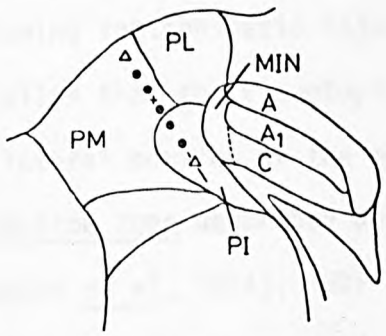


b) A 6·5

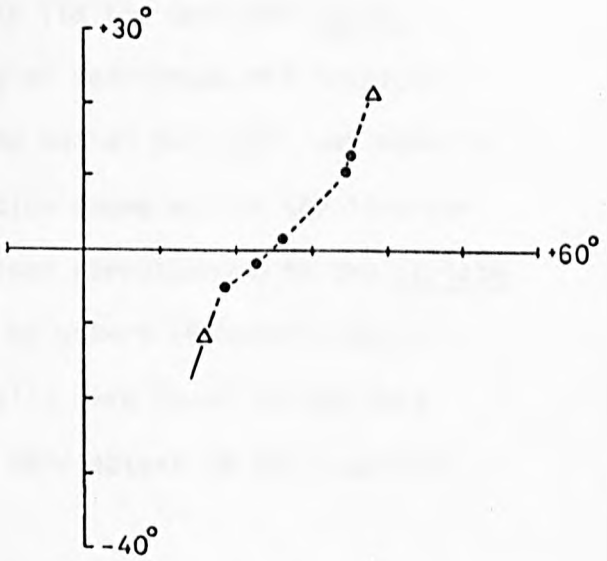




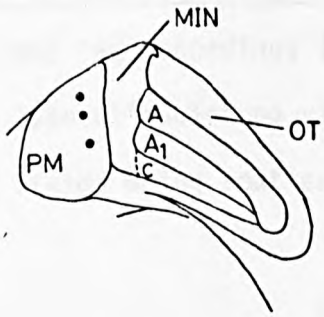
c) A 5·5

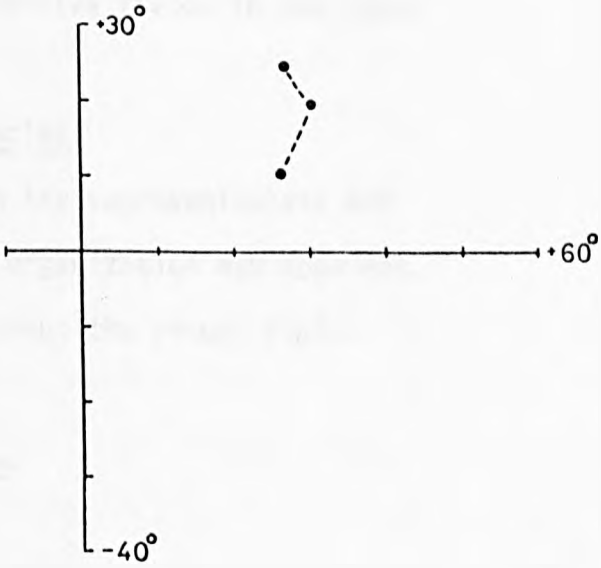


2 mm



d) A 4·5





some further investigation. Electrode penetrations directed mediolaterally confirmed that cells located more dorsally (the presumed striate projection zone) showed a more ordered visuotopic progression than those cells recorded more ventrally (in the presumed tectal projection zone). In addition, tracing of retrograde HRP transport, following iontophoretic injection in the medial pulvinar, was used to establish that the visuotopic organization found within the inferior and lateral portion of the medial pulvinar corresponded to the striate projection zone described anatomically by others (Graybiel, 1972; Kawamura et al, 1974). HRP positive cells were found in the deep layers of cortical areas 17 and 18 and were absent in the superior colliculus.

Lateral pulvinar:

During this preliminary study no visuotopic organization was demonstrable in the lateral pulvinar, although there was a tendency for many of the cells (65%) to have receptive fields in the upper visual field.

Other lateral and posterior thalamic nuclei:

From the few recordings located in the suprageniculate and posterior lateral nuclei no visuotopic organization was apparent, receptive fields being scattered throughout the visual field.

5.4. Conclusion:

Cells with similar response characteristics to those reported here have been described in cats under local anaesthesia and paralysis (Suzuki & Kato, 1969), chloralose anaesthesia (Kinston et al, 1969; Wright, 1971), in 'cerveau isole' and in pretrigeminal preparations

(Godfraind et al, 1972), and N_2O/O_2 with local anaesthesia (Palmer et al, 1975). The visually non-responsive cells, totalling 40% of the sample, may represent two populations of cells, cells with complex trigger features and/or cells which are visually non-responsive. There are both similarities and disimilarities between the receptive field types recorded in the pulvinar-complex and the cell types found in the areas which project to the pulvinar-complex. For example, many cells in the superior colliculus are directionally selective (e.g. Sterling & Wickelgren, 1969; Berman & Cynader, 1972) as are cells in the deeper striate cortical layers (Palmer & Rosenquist, 1974). Movement sensitive cells have only been reported in the superior colliculus (Berman & Cynader, 1972). The majority of cells in visual cortical areas 17, 18 and 19 have small orientation-selective/sensitive cells (Hubel & Wiesel, 1962, 1965; Pettigrew et al, 1968; Henry et al, 1974; Rose & Blakemore, 1974; Watkins & Berkley, 1974). This is contrary to the present observations in the pulvinar-complex where most of the cells had large receptive fields and only a few (7/117) were orientation sensitive. Diffuse field types appear to be unique to the pulvinar-complex. Concentric receptive field types resembled those found in the LGNd complex, in particular the 'sluggish' transient cells, which is compatible with the suggestions of an afferent projection from the LGNd complex to the pulvinar nuclei (Altman, 1962; Vastola, 1961; Bruner, 1965). There are also resemblances with some of the cells in cortical areas to which the pulvinar nuclei project. Similar cell types (diffuse, concentric, movement-, direction- and orientation-sensitive) have been described in the medial division of the CBA (Hubel & Wiesel, 1969; Wright, 1969; Spear & Baumann, 1975a) and (movement sensitive cells) in

the middle suprasylvian gyrus (presumably areas 7 and 21 - Dow & Dubner, 1971).

From the present results it appears that the projection zones from striate cortex and the superior colliculus in the inferior and medial pulvinar nuclei may be viewed as comprising two obliquely oriented columns of cells, each of which contains a coarse yisuotopic organization. This topographic organization is in agreement with anatomical reports which demonstrate a representation of the upper visual field dorsally and the lower visual field ventrally (Kawamura et al, 1974; Kawamura, 1974). These anatomical studies have also shown a third representation in the lateral pulvinar and within which no visuotopic organization was demonstrable. It is of interest to note that cytoarchitectural boundaries (in this case the inferior and medial pulvinar nuclei) do not delineate the functional (visuotopically organized) regions.

Chapter 6

NEURONAL ORGANIZATION IN THE RAT'S LGNd AND PULVINAR:

The prime objectives of studying the rat LGNd were firstly to determine whether a secondary, mirror image representation is present in this species (as suggested electrophysiologically by Montero et al, 1968), in particular through mapping the visual field contained within the medial portion of the LGNd where such a representation may be present; secondly to determine whether a sustained/transient classification of receptive field types is present in the rat as suggested from conduction velocity data (Fukuda, 1973); thirdly, if such a classification is confirmed, to determine whether the homologue of the feline MIN, if present, possesses transient cells as found for the cat.

In this discussion the visually responsive nucleus situated medially to the LGNd will be termed the 'pulvinar complex' in keeping with the previous description of the pulvinar complex in the cat, for this nucleus is also associated with the visual system projecting to extrastriate cortex (Lashley, 1941) and corresponds to the lateral posterior nucleus described by others (e.g. König & Klippel, 1963).

6.1. Visuotopic organization:

LGNd:

The visuotopic organization within the rat LGNd was assessed from both single and multi-unit activity. Electrode penetrations

were restricted, according to subsequent histology, to the middle of the LGNd in its antero-posterior extent and confined mainly to the medial third of the nucleus. Most of the units' receptive fields were located in the visual field within 40° of the intersection between the zero vertical and horizontal meridians. The zero vertical meridian was taken as the line resulting from intersection of the rat's midsaggital plane with the tangent screen; the zero horizontal meridian was levelled at the horizontal plane passing through the rat's eye.

The visuotopic organization was essentially similar to that found by Montero et al (1968) in the LGNd of the albino rat. A similar organization held for the hooded rats used during this study. The upper visual field was represented anteriorly and the lower visual field posteriorly, with the central visual field represented medially in the LGNd. Of the three albino rats used, there were insufficient data to compare the electrophysiological mapping data with the retinal projections determined anatomically for the two strains (e.g. Lund et al,1975).

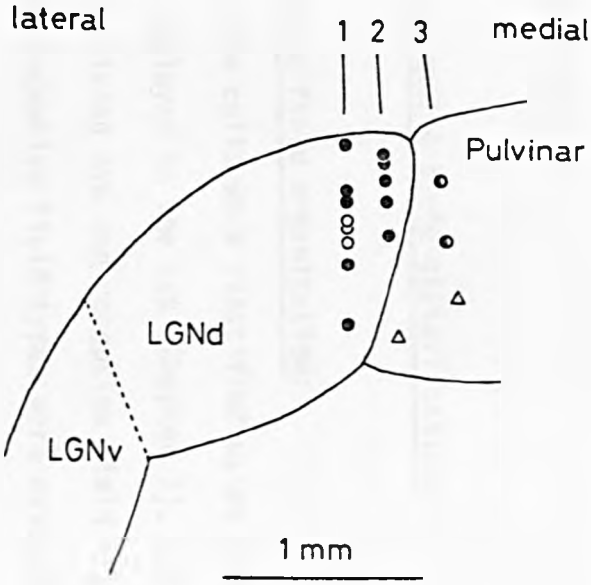
Occasionally, at the medial edge of the LGNd at the middle of its antero-posterior extent, cells were recorded whose receptive fields extended up to 20° into the ipsilateral visual field (Fig. 27). All of these cells (7/69) were found to be driven by the contralateral eye and had transient receptive field properties - see later.

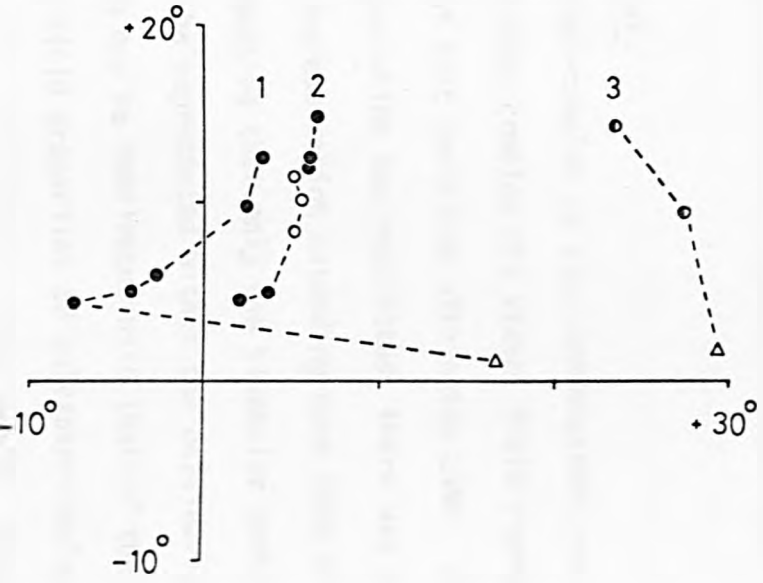
During the present study there was no evidence of a secondary representation of the visual field contained within the nuclear boundary of the LGNd. This is contrary to the report of Montero et al (1968); however, these authors described such a secondary visual representation antero-medially in the LGNd, a region rarely recorded

Fig. 27.

The locations in the LGNd and pulvinar nuclei of the rat of visually responsive cells (circles) and multiunit activity (open triangles) recorded during three electrode penetrations and the positions of their receptive field centres in the visual field. Filled circles, contralateral drive; open circles, ipsilateral drive; half filled circles binocular drive.

Rat 09




+20°
1
2
3
-10°
+30°
-10°

from during this study. Subsequent histology showed that most electrode tracks had actually passed through and entered the pulvinar-complex.

Pulvinar complex:

The pulvinar-complex is situated adjacent and medial to the LGNd. Within the pulvinar complex the visual field representation is a mirror image of that contained within the LGNd. Although investigation of this representation was restricted, there was no evidence of the visual field representation extending more than 50° from the vertical meridian, suggesting that only the binocular portion of the visual field may not be represented within the pulvinar-complex. This visual representation may be homologous with that of the feline MIN since the receptive field properties of pulvinar-complex cells resembled those of cells found in the pulvinar-complex of the cat in that they were movement and direction sensitive and only rarely elicited on-off responses to flash presentations.

6.2. Receptive field classification:

6.2.1. LGNd - Receptive field organization:

Visually responsive cells were classified using identical techniques to those employed in the cat (Chapter 3). Initially on isolating a cell the driving eye and receptive field organization were determined. The receptive field types were essentially similar to those described by Montero and colleagues for the albino rat (Montero et al, 1968; Montero & Brugge, 1969; Montero & Robles, 1971). The majority of classified cells (52/60) were concentrically organized on- or off-centre types with antagonistic surrounds, which

could be further classified as either sustained or transient. Five cells had no demonstrable surround - 'centre-only' cells. The remaining three cells had on-off receptive fields and were either direction sensitive (2 cells) for a moving bar, or movement sensitive (1 cell) in responding to bar motion in all directions.

The strength of the antagonistic surround in concentric-field cells tended to be stronger in those cells, whether sustained or transient, possessing smaller receptive field centres. For many cells the surround could only be revealed when adapting the receptive field centre with a spot of appropriate contrast while exploring the surround with a second spot. Even with this technique for five cells (5/60), (4 on- and 1 off-'centre') it was not possible to demonstrate a surround ('centre-only' cells). Similar observations have been made by others with regard to variability in the strength of the antagonistic surround at both retinal and geniculate levels (Partridge & Brown, 1970; Montero & Robles, 1971) and in demonstrating cells with apparently no surround component (Brown & Rojas, 1965; Partridge & Brown, 1970; Montero & Robles, 1971). Sefton & Bruce (1971) reported LGNd cells in which only partial surrounds could be mapped; during the present study parts of the surround were weakly represented or even absent.

6.2.2. Sustained/Transient classification:

Sustained or transient properties were assessed according to (i) response to standing contrast, with stimulus contrast appropriate to the centre; (ii) receptive field centre size; (iii) velocity selectivity, with a stimulus of contrast appropriate to the surround; and (iv) response to moving gratings. [Of 69 cells tested, 57 were

either sustained or transient - see Table 4.]

In the present report no attempt was made to distinguish between the possible occurrence of 'brisk' and 'sluggish' sustained/transient cells. The responses of sustained and transient cells in the rat LGNd were essentially similar to those of comparable cells described for the cat (Chapter 3).

Response to standing contrast:

Cells in the rat's LGNd were classified as either sustained or transient with respect to their responses to an optimally sized spot, of contrast appropriate to the receptive field centre, presented for 500 msec or 30 sec. over the receptive field centre. Cells yielded similar responses to those found in the cat; sustained cells responded with an elevated discharge for the duration of the stimulus presentation; while transient cells responded with a phasic discharge (Fig. 28). Interestingly, all of the 'centre-only' cells had sustained properties, yielding a response which, from cursory observation, appeared to be related to background intensity. Similar cells have been described in the albino rat (Montero & Robles, 1971).

Receptive field centre size:

Receptive field centre sizes were defined as contours of iso-sensitivity to small (0.5° or 1° diameter) light spots and ranged between 2.5-6° for sustained cells and 3.25-9° for transient cells, with LGNd receptive field eccentricities up to 40° from the insection between zero horizontal and vertical meridians. As found in the cat, receptive field centre size increased with increasing eccentricity.

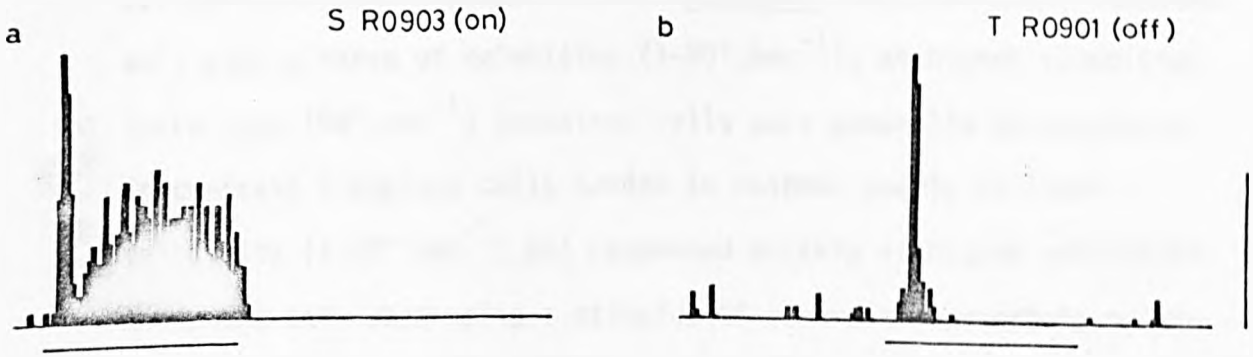
Table 4: Rat LGNd / Pulvinar-complex:

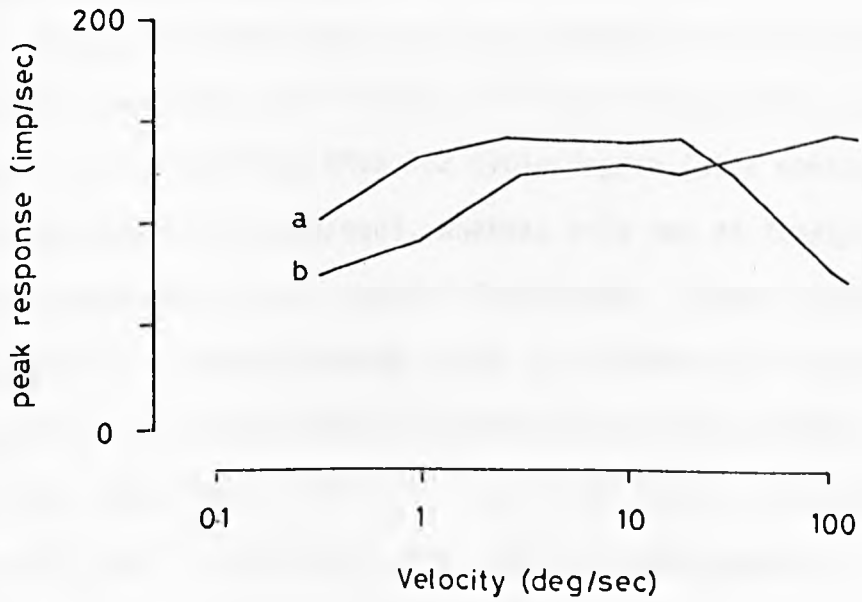
	Sustained	Transient	Direction sensitive	Movement sensitive	Diffuse	Unclassified
LGNd (contralaterally driven)	25	23	2	1	—	7
LGNd (ipsilaterally driven)	4	5	—	—	—	2
Pulvinar-complex	—	—	8	5	1	6

Fig. 28.

(upper) PSTH's for an on-centre sustained cell (a) and an off-centre transient cell (b) recorded from the rat's LGNd, accumulated over 16 consecutive presentations of an optimally sized light (a) or dark (b) square generated on the CRT display, positioned over the receptive field centre. Bin width 10.24 msec; vertical bar calibration 50 impulses/bin; horizontal bar calibration indicates a 500 msec presentation of the light (a) or dark (b) square.

(lower) Velocity tuning curves for the above cells. The stimuli were light or dark squares of contrast appropriate to the receptive surround of the given cell and approximately twice the receptive field centre diameter in size.


a
S R0903 (on)
b
T R0901 (off)


200
0
peak response (imp/sec)
a
b
0·1
1
10
100
Velocity (deg/sec)

Velocity sensitivity:

Responses to motion of light and dark bars or discs (about twice the receptive field centre diameter) over a range of velocities (1-120°.sec^{-1}) were assessed. With a stimulus of contrast appropriate to the receptive field surround sustained cells responded well over a range of velocities (1-80°.sec^{-1}); at higher velocities (more than 100°.sec^{-1}) sustained cells were generally unresponsive. In contrast transient cells tended to respond poorly at lower velocities (1-10°.sec^{-1}) but responded briskly at higher velocities. As in the cat, when using a stimulus of contrast appropriate to the receptive field centre, many sustained cells would also respond at velocities more than 100°.sec^{-1}.

Response to grating motion:

Again, responses were similar to those obtained in the cat. Of eighteen sustained cells tested, ten cells responded to motion of a parallel grating finer than 1.2 cycle/degree (at a constant temporal frequency about 1 cycle/sec), whereas only two of twenty-one transient cells responded to such spatial frequencies. When tested with movement of a coarse grating (0.82 cycles/degree) at various velocities, sustained cells responded to passage of each grating bar at slow velocities (1-20°.sec^{-1}) while at higher velocities (more than 50°.sec^{-1}) such cells were generally unresponsive; transient cells, however, at higher velocities responded with an elevated discharge which was subsequently replaced by a discharge to motion of the grating.

Other observations:

For the three anaesthetic regimes used, both sustained and transient cell types were found. Neuroleptanaesthesia was used most frequently as it appeared to give the most stable preparation, judged from cell responsiveness and the rat's physiological condition.

As mentioned in the methods section (Chapter 2) the hooded rats consisted of previously undernourished and control animals. With regard to their responsiveness to visual stimuli no differences between animals from these groups were apparent. There have been no published studies of any histological effects on the LGNd or pulvinar nuclei following pre- and/or neonatal undernutrition. However, Cragg (1972) noted that histological changes were present in the visual cortex (area 17) of such animals.

6.2.3. Distribution of receptive field types:

The distribution of cell types in the rat's LGNd is shown in Table 4. Contralaterally and ipsilaterally driven cells dorso-ventrally in the LGNd show some semblance of layering, with ipsilaterally driven cells sandwiched between contralaterally driven layers - see Fig. 27. While ipsilaterally driven background activity was apparent in most of the rats studied it proved difficult to isolate single cells.

The movement sensitive cell and the two direction sensitive cells were contralaterally driven. These cells were located ventrally in the LGNd, i.e. ventral to the ipsilateral 'layer'. 'Centre-only' cells (5/69) were also recorded ventrally in the LGNd and all were driven contralaterally. Sustained and transient cells were found throughout the LGNd.

6.3.1. Pulvinar-complex - Receptive field types:

Of the twenty cells isolated within the pulvinar-complex, receptive field properties were described for fourteen - see Table 4. These resembled receptive fields in the pulvinar-complex in the cat (see Chapter 5) and the cells were again distinguished from geniculate cells by their poor responsiveness to flashed stimuli, preference for moving stimuli and in being driven by either eye. There are insufficient data at present for detailed comparisons with the cat.

Conclusion:

The present data indicate that, like the cat, the rat has parallel and distinct sustained and transient systems at the geniculate level. Previous conduction velocity measurements by Fukuda and colleagues (Fukuda, 1973; Fukuda & Sugitani, 1974) have also implicated two classes of cells. Moreover, inspection of PSTH's to flashed stimuli in the published figures of many authors (Montero & Robles, 1971; Sefton & Bruce, 1971) suggests sustained- or transient-like responses. Hughes (1974), in a brief abstract, has also reported the existence of sustained, transient and direction-sensitive cells in the rat's optic tract.

Although no distinction was made between 'sluggish' and 'brisk' types there was some suggestion that both types may be present. The response characteristics of the sustained 'centre-only' cells resembled those of some 'sluggish' sustained cells found in layer C and C_1 of the cat's laminated LGNd (Mason, unpublished observations) in that their discharge appeared to be proportional to the background

intensity. Similar cells ('luminance units') have been described in more detail by others in the cat's retina (Barlow & Levick, 1969; Stone & Fukuda, 1974). These cells, and the direction and movement sensitive cells, were recorded from the ventral contralateral 'layer'; it should be cautioned that these observations are based on a small cell sample. Interestingly, other authors have noted a similarity between the organization of the LGNd in the rat and the cat (Cunningham & Lund, 1971; Lund & Cunningham, 1972). Lund & Cunningham (1972) suggested that the outer layer (comprising the dorsal contralateral layer and the ipsilateral layer) is comparable to the A-laminae of the cat, while the inner layer (the ventral contralateral layer) is comparable to the C laminae of the cat. Furthermore, Kriebel (1975) has classified rat LGNd neurones into three types (types 1, 2 and 3) and has suggested that types 1 (large-sized somata) and 2 (medium-sized somata) represent two types of relay cells (possibly corresponding to the transient and sustained cells described here) and that type 3 neurones (small-sized somata) may represent inhibitory interneurones.

The existence of a secondary visual field representation within the rat LGNd was not apparent from this study. A comparison between any differential distribution of cell types was not therefore possible. However, Montero et al (1968) did hint that the secondary representation they found in the rat might be extrageniculate in origin (a similar suggestion was made by Hughes (1971) with regard to the secondary representation found in the rabbit). The secondary mirror representation found during this study was confined within the pulvinar-complex adjacent to the LGNd. The cell responses were different from those found in the LGNd which is consistent with the

absence of retinal afferents to the pulvinar-complex (e.g. Lund et al, 1975).

Although a homologue of the feline MIN was not found, the group of cells exhibiting large nasotemporal overlap (up to 20° into the ipsilateral visual field) and possessing transient receptive field properties resembled those which, in the cat, were regarded as constituting the medial limb of layer C. Such cells in the rat were situated on the medial ridge of the LGNd in the middle of its antero-posterior extent, an arrangement which suggests that it may be a homologue of the medial limb of layer C in the cat. Lund et al (1975) noted that, in pigmented rats with retinal lesions temporal to the decussation line, in addition to degeneration in the ipsilateral LGNd there was a wedge of degeneration on the dorsomedial border in the contralateral LGNd.

Chapter 7 DISCUSSION - AN OVERVIEW:

LGNd-complex:

One of the objectives of this thesis was to investigate the distribution of receptive field types within the nuclei which comprise the LGNd complex, notably the laminated LGNd and MIN. During initial studies (LGNd-complex study I) the response properties of cells in the MIN were compared with those in the laminated LGNd, with respect to the sustained/transient classification. This study revealed that the proportion of transient cells in the MIN (86%) is higher than in the laminated LGNd (42%). Those sustained cells which were present in the MIN were located along the lateral edge of the MIN adjacent to the laminated LGNd; such sustained cells were also contralaterally driven. With the exclusion of this lateral marginal region, virtually all cells within the MIN have transient properties. It may also be argued that the lateral margin of the MIN is an extension of layer C in that the cells resemble those found in layer C in being contralaterally driven, exhibiting a large nasotemporal overlap (more than 3°, in comparison to that found in layer A cells which never exceeds 2°) and having a similar distribution of sustained and transient cells (37%: 61% compared to 45%:54% sustained: transient respectively) representing a similar area of the visual field. These results are compatible with Guillery's re-evaluation of earlier anatomical data (see Chapter 1) in which he regards the lateral margin of the MIN as the medial limb of layer C of laminated LGNd.

Using oblique electrode penetrations, a partially overlapping arrangement of ipsilaterally and contralaterally driven cells may

be revealed. This includes a contralaterally driven group of cells located at the MIN-laminated LGNd border, the majority of which are transient (32/52 - study I) and exhibit a large nasotemporal overlap; an ipsilateral driven group of cells occupying a central position in the MIN which are almost exclusively transient; and a contralaterally driven group of cells located along the medial edge of the MIN, all with transient properties. The contralaterally driven cells along the lateral margin of the MIN were considered to constitute the medial limb of layer C. This evidence is thus consistent with the MIN being a bi-laminar structure within which virtually all cells have transient properties. Independently, Dreher & Sefton (1975) and Palmer et al (1975) showed that most cells in the MIN have transient (Y) properties, and Dreher & Sefton also noted that some sustained (X) cells were located at the MIN/laminated LGNd border, these observations being in agreement with the present study (and Mason, 1975).

During the course of the study, reports further subclassifying sustained and transient retinal ganglion cells as either 'brisk' (X or Y cells) or 'sluggish' (concentric W cells) types became available (Cleland & Levick, 1974a, b; Stone & Fukuda, 1974). It was noted during the present study, in agreement with others (Hubel & Wiesel, 1961; Daniel et al, 1962) that many cells recorded from layers C and C_1 were different from those in the A layers. Such cells were, in general, less responsive to visual stimuli and tended to possess receptive field centres greater than 2° in diameter. This resemblance to 'sluggish' cell types prompted a re-investigation of the response properties of cells in the LGNd complex, in particular those cells found in the C layers. This revealed a differential

distribution of 'brisk' and 'sluggish' cell types within the LGNd complex. 'Brisk' sustained and transient cells were recorded from layers A, A_1 and C ('brisk' transient cells predominating in the upper (magnocellular) portion of layer C); while 'sluggish' sustained and transient cells were located in the lower (parvocellular) portion of layer C and in layer C_1; the MIN contained almost exclusively 'brisk' transient cells. It is of interest that the magnocellular regions of the LGNd complex (i.e. the MIN and upper portion of layer C) contain predominantly 'brisk' transient cells while in the parvocellular regions (layer C_1 and the lower portion of layer C) 'sluggish' cell types predominate. This relationship between cell somata size and receptive field type is compatible with the correlation between receptive field type and cell morphology established in the cat's retina (Cleland & Levick, 1974a, b; Cleland et al 1975). Independently, Wilson & Stone (1975) and Cleland and co-workers (1975, 1976) have also reported 'sluggish' (W-cell) types in the C-layers of the cat's LGNd; Cleland et al (1975, 1976) also claimed to have found a few 'sluggish' cell types in the A layers.

Many early anatomical studies have described a magnocellular layer ventral to layer A_1, corresponding to the upper (magnocellular) portion of layer C described here, (Thuma, 1928; Rioch, 1929; Kanaseki, 1958; Guillery, 1970) which will be referred to as the CIN (after Thuma, 1928). As argued from evidence from this study, presented in Chapter 3, the CIN was redefined as comprising the magnocellular portion of layer C and the lateral margin of the MIN (i.e. the medial limb of layer C).

When comparing the neuronal organization found in the cat's LGNd complex with that of other species whose visual systems are well

developed, many similarities are present. With primates as an example (the rhesus monkey specifically) the LGNd shows a distinct lamination composed of layers 1-4 containing medium-sized cells (frequently termed the 'parvocellular layers'); the magnocellular layers (layers 5 and 6); and a parvocellular layer (i.e. layer S according to Campos-Ortega & Hayhow, 1970). This is very similar to the situation found in the cat, viz layers A and A_1 containing medium-sized cells, magnocellular layers (the MIN and CIN) and parvocellular layers (layers C_1, C_2 and C_3). The differences in histological and physiological organization between these species may well be related to differences in their visual behaviour. With regard to physiology, the rhesus monkey exhibits a differentiation of sustained and transient cells in the LGNd: sustained cells, generally exhibiting colour opponency, are located in the layers of medium-sized cells while transient cells, with little or no colour opponency, are found in the magnocellular layers (Dreher et al, 1976). No physiological data on the parvocellular layers S are available. Similarly, transient cells have been recorded from the cat's magnocellular layers (the MIN and CIN) while, in contrast, both sustained and transient cells are located in the cat's medium-sized cell layers (A and A_1). These results suggest that, in the rhesus monkey, chromatic and spatial information is dealt with by the sustained pathway via the layers of medium-sized cells whereas other (e.g. temporal) information are dealt with through the transient pathway via the magnocellular layers. The few colour-sensitive cells reported in the cat are located in the parvocellular layers and their receptive field properties appear to be different from those found in the rhesus monkey (Daw & Pearlman, 1970; Wilson & Stone, 1975;

Cleland et al, 1976). However, similar colour-sensitive cells may be present in layer S of primates, or alternatively, these colour-sensitive cells may be unique to the cat and possibly other carnivora.

A study of the responses of cells in the LGNd complex to static visual noise was undertaken to establish (a) whether the cell types present at the geniculate level were differentiated similarly to the simple and complex cells of the visual cortex and (b) whether use of textured stimuli might reveal a differential responsiveness associated with the individual nuclei of the LGNd complex. On-centre/off-centre and sustained/transient cell types in the LGNd complex were not differentiable by their responsiveness to textured stimuli, unlike the simple and complex cells in the striate cortex (Hammond & MacKay, 1975a,b; 1976). This result suggests that the differential responsiveness at the cortical level must be due to intra-cortical processing rather than to selectivity at earlier stages in the visual pathway. Furthermore, there was no distinction in responsiveness to visual texture between cell types from the constituent nuclei (i.e. the laminated LGNd and the MIN) of the LGNd complex.

In contrast to the laminated LGNd complex found in the cat, the rat's LGNd shows no lamination in histological material and no evidence of segregation of cells of differing somata diameter (i.e. no evidence of medio-, magno- and parvocellular organization). Within the rat's LGNd both sustained and transient cells were found although, in agreement with the histology no histological differentiation of sustained or transient cells was found. This is in contrast to the organization found in the cat (i.e. between the laminated LGNd and the MIN - present study; Mason, 1975; 1976a) and in primates (Dreher et al,

1976). Furthermore, no homologue of the feline MIN could be found in the rat.

Functional significance of the MIN:

In earlier anatomical studies both Hayhow (1958) and Stone & Hansen (1966) tentatively suggested possible functions for the MIN in the processing of visual information. Hayhow (1958) concluded that the retinal overlap found in the MIN may indicate that MIN neurones receive binocular input, so providing a clue to the significance of the nucleus. However, only a small proportion of binocularly driven cells were isolated during the present study (2/179 from the bilaminar MIN), which is in agreement with other reports (Kinston et al, 1969; Sanderson, 1971). It therefore seems unlikely that the MIN has any role in binocular vision distinct from that of the laminated LGNd. An absence of central representation in the MIN, reported by Stone & Hansen (1966), suggested to them a role essentially concerned with peripheral vision. More recent anatomical (e.g. Garey & Powell, 1968) and physiological mapping studies (Sanderson, 1971) revealed that central vision was in fact represented at the laminated LGNd/MIN border in the middle of its anteroposterior extent. During this study, cells whose receptive fields were within 2° of the area centralis tended to be contained within the medial limb of layer C.

Although previously regarded as a thalamic relay for the afferent projection to extrastriate cortex, its small size (and hence small population of cells) compared with the laminated LGNd suggests that the MIN cannot provide a major projection to areas 18, 19 and the medial division of CBA. This probably accounts for the weaker

labelling of cells in the MIN, compared with the laminated LGNd, following retrograde transport of HRP injected in area 18 (an observation also noted by Maciewicz, 1975). Tretter and colleagues (1975) suggested that area 18 of the cat's visual cortex should be regarded as a primary, rather than as a secondary visual area, being organized in parallel with area 17. Further recent observations demonstrate that ablation of area 17 has little affect on many of the receptive field properties of cells in area 18 (i.e. receptive field size, orientation tuning, velocity preference, and the proportions of orientation and direction selective cells - Dreher & Cottee, 1975), indicating that these properties are determined by the thalamic input rather than by cortico-cortical connections. The diffuse projection from the MIN to extrastriate cortex mentioned earlier is suggestive that the nucleus may have a widespread role in extrastriate physiology. This may manifest itself as a distinct sub-class of cortical neurones with particular properties and/or connections (for example as demonstrated for corticotectal complex cells in layer V of area 17 - Palmer & Rosenquist, 1974). However, during the present study no differences between transient cells found in the MIN and in the laminated LGNd were found.

The functional significance of the MIN may be hinted at by comparative studies of other mammalian species for which possible homologues of the MIN have been described. Criteria which characterize the feline MIN and so establish a definitive homology are:

(i) a bilaterally innervated retinal projection field, situated medial to the laminated LGNd;

(ii) a visuotopic organization of this area arranged as a mirror-image of that present in the laminated LGNd;

(iii) a retinotopic projection to extrastriate cortex;

(iv) a magnocellular cell group with transient-like properties.

Only for a limited number of species has a discrete nucleus, presumed to be homologous to the feline MIN, been described anatomically. This comprised a magnocellular cell group situated medial to the laminated LGNd in a variety of Carnivore families (Sanderson, 1974) and ungulate species (e.g. Karamanlidis & Magras, 1972; 1974) which, following eye enucleation, reveals a bilaminar organization. Secondary visual field representations have been described in the rabbit (Choudhury & Whitteridge, 1965; Hughes, 1971) and in the rat (Montero et al, 1968), although it has been suggested that these secondary visual representations may be of extrageniculate origin (Hughes, 1971; the present study).

Two possible candidates for presumptive homologues of the feline MIN have been suggested in primates.

(i) A bilateral retinal projection, restricted to a rostral portion of the inferior pulvinar (adjacent to the laminated LGNd), has been described only in Old World primates (Campos-Ortega et al, 1970; Trachtenberg, 1974). The significance of this extrageniculate retinal projection field awaits further investigation with regards its cortical projections (if any) and whether a separate representation of the visual field is present. Of interest are the reports of similar restricted retinal projections to the pulvinar- complex adjacent to the LGNd in a number of sub-primate species e.g. hedgehog (Hall & Ebner, cited by Snyder 1973), hamster (Schneider, 1973) and cat (Hedreen, 1970). It is possible that these observations are the

result of anomalous retinal connections during development (see Schneider, 1973).

(ii) A second extrageniculate retinal projection field has been described in both New and Old World primates (Minkowski, 1920; Polyak, 1957; Kanagasuntheram et al, 1969; Campos-Ortega & Hayhow, 1971; Tigges & O'Steen, 1974; Hendrickson et al, 1975 - see Chapter 1). This comprises a bilateral retinal projection to a cell group situated medial to the LGNd and the parvocellular cell group appears to be discrete from that of the pregeniculate nucleus (PGN). Little is known of the extent of the representation of the visual field in this cell group or of its cortical connections (although Campos-Ortega & Hayhow (1971) suggested only the lower visual field might be represented; these authors also found no cortical projection to the lateral striate or extrastriate cortex, although the possibility of a projection to the medial surface remains). It is possible that this retinal projection field may be, more appropriately, homologous to the recently described bilateral retinal projection field wedged between the LGND and LGNv in the rat - the intergeniculate leaflet (Lund et al, 1975; Hickey & Spear, 1976).

An alternative view may be that in some species the MIN homologue remains undifferentiated from the LGNd (as Hayhow argued for the marsupial phalanger - Hayhow, 1967), being contained within the magnocellular region of the LGNd. It may be that in those species which exhibit a differentiated MIN, as in the cat, they may also show a similar organization in their visual cortex in that a portion of extrastriate cortex resembles that of a primary rather than a secondary visual area; evidence for this is lacking at present although for another carnivore, the mink, there is a suggestion that

a similar organization to that found in the cat may exist (Sanderson & Kaas, 1974). As argued in the present study (and suggested earlier by Thuma, 1928), the MIN in the cat may be regarded as comprising a differentiated portion of a magnocellular lamina of which the CIN remains within the laminated LGNd. No differences between the 'brisk' transient cells found in the MIN or CIN were found with the exception of the mirror-image representation of the visual field present in the MIN. In addition no differences were found with regard to the projections from the MIN and CIN to area 18, demonstrated using retrograde HRP tracing. It is probable that this differential projection of the cat's 'magnocellular layer' (the MIN and CIN) may be a reflection of a difference in neuronal organization associated with the suggestion that the cat may possess two 'primary' visual cortical areas (areas 17 and 18). Hubel & Wiesel (1972) demonstrated a differential laminar projection from the mediocellular and magnocellular layers of rhesus monkey LGNd to different layers in the striate cortex following discrete lesions to individual layers. Similar laminar organization of geniculate afferents has been reported in the tree shrew, bushbaby and owl monkey (Harting et al, 1974; Glendenning et al, 1976; Kaas et al, 1976). A similar situation may also hold for cat with regards the MIN and CIN, with the exception that it involves a different cortical area, although this does not exclude the possibility that a differential projection to different cortical layers may also be present. Recently, LeVay & Gilbert (1976) described the projections from the cat's laminated LGNd (layers A, A_1 and the C-layers) to striate cortex, showing a differential laminar projection of layers A and A_1 compared with the C-layers. The individual sub-layers of layer C were not distinguished; however, from

the absence of projections from the CIN to area 17 noted in the present study, the laminar projection reported by LeVay & Gilbert may be almost entirely due to the parvocellular portion of the C-layers. This differential laminar projection found in the striate cortex for a number of species is no doubt associated with differences in the processing of visual information. For example, layer VI contains cells which give rise to the cortico-geniculate pathway, suggesting that a monosynaptic recurrent mechanism may be operating, while the separation of mediocellular (sustained cells) and magnocellular (transient cells) geniculate projections in cortical sub-laminae in layer IV suggests that discrete cortical cell populations may be responsible for processing different aspects of visual information (via sustained and transient geniculate afferents).

The present proposal that the feline homologue of the MIN in some species may be associated with the magnocellular portion of the LGNd of those species is further supported by comparing the functional connectivity of the cortico-fugal pathways to the LGNd complex of the cat with that of primates. In the cat, corticofugal projections to the MIN and CIN originate from extrastriate cortex (areas 18 and 19), while those to the laminated LGNd originate from areas 17 and 18 (Niimi et al 1971; Kawamura et al, 1974). Similarly in the owl monkey and rhesus monkey, extrastriate cortex (V2 and MT) has been reported to project to the magnocellular layers in the LGNd (Lin, 1976; Wong-Riley, 1976).

This suggestion that the feline MIN has differentiated from the magnocellular region in laminated LGNd, of which the CIN remains, also explains earlier suggestions as to the significance of the MIN. The significance of the binocular overlap of retinal afferents in the

MIN has already been discussed in section 3.4.2. Without such overlap, portions of the visual field represented in the MIN would be devoid of representation by either the contralateral or ipsilateral eye, due to the arrangement of visual field azimuth and elevation in the MIN. Secondly, whether the MIN is concerned with peripheral vision (Stone & Hansen, 1966) is dependent on one's definition of the extent of the MIN. The bilaminar MIN as defined in the present study does contain, primarily, a representation of the peripheral visual field, while that of the CIN (which includes the medial limb of layer C) contains a complete representation of the visual field with the central visual field contained largely within the medial limb of layer C. On the view that the MIN and CIN form a magnocellular entity (in which the MIN may be regarded as having 'flipped' through 180° to mirror the CIN), then its role includes both central and peripheral vision.

Pulvinar-complex:

As discussed earlier in the introductory review, one of the major obstacles confronting investigations of the pulvinar-complex, particularly when comparing results from different species, is the inconsistencies of nomenclature present in the literature. It was also argued earlier that connectivity pattern studies provide evidence for a functional division of the pulvinar-complex, which may not reflect that obtained using cytoarchitectural criteria. This is exemplified in the organization of the cat's pulvinar-complex. In an attempt to unify the nomenclature used for the thalamus, Niimi and Kuwahara (1973) in their cytoarchitectural study, subdivided the pulvinar-complex into the inferior, lateral and medial pulvinar

nuclei* (see Chapter 1) and inferred homologies, as other authors have, directly with similarly named nuclei in other species, particularly primates - with which most of this comparison will be concerned. However, the organization of the visual field representation found in the pulvinar-complex during this study is incompatible with its being contained within nuclear boundaries; this is supported by connectivity pattern studies (Graybiel, 1972; Kawamura et al, 1974; Kawamura, 1974). From Chapter 5 it will be noted that two representations of the visual field have been described in the pulvinar-complex, one extending through the inferior and medial pulvinar nuclei and the other, situated ventral to the former, contained within the medial pulvinar. The cells forming the inferior-medial pulvinar representation possessed similar receptive field types and were correlated with the striate projection zone, established using retrograde tracing of HRP transport. The cells of the more ventral medial pulvinar representation were presumed to be contained within the tectal projection zone. The cortical projections of these zones, at least to the CBA, are different, with the tectal zone projecting to the lateral division of the CBA and the striate zone to the medial division. Clearly, cytoarchitectural boundaries, i.e. the inferior and medial pulvinar nuclei, do not necessarily delineate

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* Footnote

A further subdivision of the pulvinar-complex, the oral pulvinar nucleus, is described in some primates (Olszewski, 1952; Gergen & MacLean, 1962). However, the oral pulvinar appears to be related to the somatosensory system (De Vito, 1971; Roppolo et al, 1973) and will not be considered further.

functional (i.e. visuotopically organized) regions; therefore, caution should be taken when comparing cytoarchitecturally defined thalamic regions between species; rather, 'functionally equivalent' regions should be compared.

Comparisons of the projections of the striate cortex and superficial layers of the superior colliculus (i.e. the tectal projection zone) may be made between species. One point of interest is that those species which use vision extensively in their behaviour tend to show complete, or near-complete, segregation of striate and tectal afferents whether their pulvinar-complex can be differentiated cytoarchitecturally (e.g. cat, tree shrew, bush baby, squirrel monkey and rhesus monkey) or not (e.g. the marsupial phalanger and grey squirrel), while those species which rely less on vision have overlapping striate and tectal projections, and a cytoarchitecturally undifferentiated pulvinar-complex (e.g. rat and hedgehog). In those species with a cytoarchitecturally differentiated pulvinar-complex (exemplified by the primates for comparison with the cat), both the striate and tectal projection fields are contained within the inferior pulvinar. This suggests that the 'functional equivalent' of the primate inferior pulvinar in the cat comprises both the inferior and medial divisions of the pulvinar-complex.

Thus the cat appears to have, functionally, only two sub-divisions of its pulvinar-complex, the striate and tectal projection zones in the inferior and medial pulvinar nuclei (which appear functionally equivalent to the primate inferior pulvinar), and the lateral pulvinar nucleus. From the evidence available, the cat's lateral pulvinar resembles both the primate lateral and medial pulvinar nuclei. The cat lateral pulvinar receives cortical afferents from areas 19, 21 and

the CBA, and projects to parieto-temporal cortex (areas 20, 21 and 7); similarly, the primate lateral and medial pulvinar nuclei have reciprocal connections with parieto-temporal cortex, although the medial pulvinar also projects to frontal and orbital cortices - no comparable projections have been described in the cat. Any homology between these nuclei is not resolved by examining sub-cortical projections to the pulvinar-complex, notably those of the prectectum. In the cat the pretectum projects to the lateral pulvinar (Graybiel, 1972) while, in primates, the pretectum does not appear to project to the visual thalamus at all (Glendenning et al, 1975; Santos-Anderston, 1976). It is probable that there is no counterpart of the primate medial pulvinar in the cat and other sub-primate species. This may well be related to the voluminous expansion of the primate pulvinar-complex, particularly the medial nucleus, which accompanies that of the parieto-temporal cortices. In some of the lower primates, e.g. the bush baby and owl monkey, only two cytoarchitectural divisions of the pulvinar-complex (the inferior and superior nuclei) have been described, which bears some resemblance to the situation found in the cat where two functional divisions of the pulvinar complex are present. The efferent projections of the bush baby's pulvinar-complex have been studied in some detail (Glendenning et al, 1975), which allows for comparison with the cat. As in cat, two functional divisions of the bush baby's inferior pulvinar, the tectal and non-tectal (presumably striate) projection zones, also project to different cortical areas (the middle and ventral temporal visual areas respectively) which may be homologous to the lateral and medial divisions of the cat's CBA on functional connectivity criteria. No projection to area 18 (V II) was present in the bush baby, which is

different from the situation found in other species, both primates and sub-primates, studied to date. However, Glendenning and co-workers (1975) noted that the superior pulvinar projects to area 18 in addition to area 19, and also to other visual areas adjacent to the middle temporal visual area. There are as yet insufficient data to imply any subdivision of the superior pulvinar. This discrepancy between the bush baby and other species again may reflect the notion that cytoarchitectural boundaries do not necessarily correlate with thalamic nuclei defined by 'functional connectivity'.

Functional significance of the pulvinar-complex

The functional significance of the pulvinar-complex is at present unclear. A major contributory factor is the lack of any uniformity in nomenclature used in defining thalamic regions and hence a problem in comparing evidence from different sources. Visual processing apart, clinical studies, involving stereotaxic surgery for relief of Parkinsonian symptoms, have implicated the pulvinar-complex in speech mechanisms (Penfield & Roberts, 1959; Ojemann et al, 1968; Van Buren, 1969). Other authors have suggested that the pulvinar-complex plays a role in pain appreciation (Kudo et al, 1966; Kudo & Yoshii, 1968; Richardson, 1967; Richardson & Zorub, 1970), again evidence provided during human stereotaxic surgery. A problem with such studies is verification of the surgical lesion sites which, fortunately for the patients, are generally not available. In those cases where such evidence is available, any comparison with sub-human primates is perplexing, as comparable data of the connectivity in man are lacking. Furthermore, there is the caution already emphasised above that cytoarchitectural and functional thalamic boundaries are not

necessarily equivalent and there is the additional possibility that the surgical lesions may have involved extrapulvinar nuclei.

More recently the pulvinar and/or the posterior lateral nuclei have been implicated in motor function, following surgical relief of various disorders of posture and movement (Cooper et al, 1971; 1973; 1974). It has been suggested the mechanism affected by such pulvinar lesions is a direct change of α - motoneurone activity (Lieberman et al, 1974). This might be through interruption of a pathway from the cerebellar fastigial nuclei (which also receives input from the deep layers of the superior colliculus - Angout & Bowsler, 1970) to the pulvinar-complex, recently described electrophysiologically in the cat (Snider & Sinis, 1971) - however, a similar pathway in primates, including man, has yet to be demonstrated. An alternative pathway by which pulvinar lesions might affect posture and motor function is that from the pulvinar-complex to the basal ganglia (i.e. the caudate and putamen nuclei), which has been described in the cat (Graybiel, 1972a) and tree shrew (Harting et al, 1973). In the cat this pulvinar-caudate pathway is restricted to the lateral edge of the 'head' of the caudate nucleus (Graybiel, 1972a), which is separate from the other visual projections of the visual cortex, exclusively to the 'tail' of the caudate nucleus. The pulvinar area which receives input from caudate nucleus is also the area where visual responses to diffuse flashed stimulation have been reported (Sedgwick & Williams, 1967; E.M. Sedgwick, personal communication). During the course of this study, this region of the caudate nucleus was explored during two microelectrode penetrations and in three cells (3/11), visually responsive receptive fields similar to those found in the cat's pulvinar-complex were described - two diffuse and one movement-sensitive field.

Little appears to be known of the involvement of the pulvinar-complex in visual processing. Hassler & Wagner (1965) reported two cases of human congenital anophthalmia in which the pulvinar-complex, particularly the inferior nucleus, was greatly reduced in volume, implying visual associations. Also, in patients with vascular or neoplastic lesions of the pulvinar-complex, although such lesions are rarely confined within a discrete thalamic region e.g. the pulvinar, visual disturbances are reported (e.g. Winkler, 1911), that often resemble those exhibited by patients with parietal damage (e.g. visual neglect - see Mountcastle et al, 1975), probably indicative of functional connections between these regions. There is little evidence from behavioural studies in animals as to the role of the pulvinar-complex in vision. Ablation studies in primates produce little or no detectable deficit in performance (Chow, 1954; Miskin, 1972; Christensen et al, 1975; Trachtenberg & Gower, 1974). It is possible that the pulvinar may be involved in directing visual attention, for while cells recorded from monkey inferotemporal cortex of animals with pulvinar lesions animals rarely exhibit discrete receptive fields, other response properties appear similar to those of normal monkeys (Gross, 1973). This possibility gains some support from suggestions as to the role of the superior colliculus, which projects to part of the pulvinar-complex (the inferior pulvinar), and which may be concerned with orientation and localization functions, particularly involving eye movements (e.g. Goldberg & Wurtz, 1972; Wurtz & Goldberg, 1972). The directing of visual attention may also involve other cortical projection areas of the pulvinar-complex, i.e. extrastriate and parietal cortices, for which neuronal correlates of visual attention mechanisms have

been reported (e.g. parietal cortex - Straschill & Schick, 1974; Mountcastle et al, 1975). That the majority of receptive field types found in the pulvinar-complex are direction or movement sensitive, as found in the present study, is encouraging in this respect and prompts further investigation, particularly in the awake, behaving animal of the association between neuronal responses in the pulvinar and eye movements. A further problem is whether or not the constituent nuclei of the pulvinar-complex are interconnected, and whether the different afferent projections (i.e. those from striate cortex and superior colliculus) remain separate and thence project in a parallel fashion to the same or functionally different cortical areas? Recently, Trojanowski & Jacobson (1975) were unable to find any evidence favouring connectivity between the constituent nuclei of the pulvinar-complex. That the striate and tectal projection zones in the pulvinar-complex are anatomically (and possibly functionally) discrete is suggested by a recent behavioural study showing a differential effect resulting from lesions in the cortical projection areas (the middle and ventral temporal visual areas) of these zones in the bush baby (Wilson et al, 1975). The pulvinar-complex could well serve a variety of functional roles.

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